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PASTURE STUDIES X. SUCCESSION AND VARIATION IN THE BOTANICAL COMPOSITION OF PERMANENT PASTURES¹

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The investigation of the botanical composition of the permanent pastures, which occupy such a large proportion of the agricultural land in the Eastern Townships of Quebec, has been carried on in conjunction with pasture improvement experiments established in 1931 by Macdonald College. Results already obtained indicate that productivity of depleted grazing areas can be substantially increased by proper management (9). The chief effect of the application of fertilizers is the greater yield of herbage (26). The increase in quantity is, moreover, accompanied by an increase in quality as measured by chemical composition (37) and nutritive value (8). Since species of plants differ greatly in their contributions to both yield and quality of herbage, the botanical composition becomes fundamental in determining the worth of pastures. The study of the flora and its complex relationships with environmental factors—climatic, physiographic, edaphic, and biotic—therefore, is a necessary preliminary to the formulation of sound rules for pasture management.

ECOLOGICAL CONCEPT OF SUCCESSION

Natural Vegetation

The study of plant communities and their interactions with the environment has led to the realization that all vegetation is *dynamic*. On an unoccupied area a certain group or "association" of plants will take hold, flourish for a time and then decline. In due course it will be succeeded by an association of entirely different composition which in turn will decline, to be followed by another, and so on, each association modifying its environment in such a manner as to make it more ameliorative to the succeeding one. Is there, then, no termination to this inevitable sequence?

Ultimately an association will be arrived at which on reaching its highest development will not decline and will not be superseded. Vegetation is then spoken of as *static* and the association, now composed of those plants best adapted to the climate and soil, as the *climax formation* or simply *climax*. Within a region of uniform climate definite species characterize the climax vegetation. In the Eastern Townships these are aborescent, an admixture of deciduous and coniferous forms, with their accompanying shrubby and herbaceous species.

¹ Part of a thesis entitled "Ecological Aspects of the Pasture-conditioned Climax in the Eastern Townships of Quebec," presented to the Faculty of Graduate Studies and Research of McGill University in partial fulfillment of the requirements for the degree of Master of Science, May, 1935.

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The concept of orderly succession leading up to stabilization one might suppose to be over-stressed and mainly deduced theoretically, since to-day regions at the climax are rarely to be found. This is due, however, to their obliteration by human agency so that vegetation in the developmental stages actually occupies nearly the entire area. Nevertheless, it is undoubtedly manifest that the tendency of succession is operative and always in an orderly and progressive direction, namely, towards the association best adapted to the prevailing conditions. The climax, once attained, is permanent as long as the environmental conditions remain constant. Over geological periods, it is true, the climatic conditions and physiographic features have changed remarkably and are still changing. The flora has become modified accordingly, but such changes have been so slow as not to be perceptible in a human lifetime and need no further mention in the present discussion.

Pasture Vegetation

A replica of the above process takes place under pasturing conditions. The succession here is progressive also and, although extremely rapid in comparison, always proceeds in the direction of, and tends to stabilize in, an association of plants best adapted, morphologically and physiologically, to the conditions. This association, too, remains at balance only as long as the pasturing remains constant. It is very susceptible to environmental changes such as the addition or deletion of factors or an increase or decrease in the intensity of already operating factors. Thus by a change in the strength of any single factor, such as, for example, an increase in the plant nutrients in the soil resulting from an application of fertilizers or an increase in grazing due to over-stocking, the delicate balance is disturbed, initiating a whole cycle of changes in vegetation which, eventually, will come to stabilization again, this time in a new and modified state such as will be most suitable to the new conditions.

Although analogous in many respects, the climatic climax, the resultant of a natural environment, and the pasture climax, the resultant of an artificially induced environment, should not be classified in the same category. It seems preferable to qualify these by distinctive terms. Certain workers (41) have been prone to use "sub-climax" for any association representing an imperfect stage where development has been arrested due to recurrent action of natural or artificial agencies. The succession controlled by such agencies is sometimes considered to be "retrogressive," the degree of retrogression and the level of re-stabilization being determined by the intensity of action of the agent. Due to heavy grazing, on the grassland climax vegetation of the prairie regions for example, the natural species are quickly exterminated and replaced by a ruderal and open community characterized by species of a primitive stage in development (31). Since the vegetation of pastures in Quebec is not a formation identical in composition or origin with any stage in the natural development of climatic climax, but is the termination of a deflexed, and progressive, succession kept distinct from the very first and stabilized under the control of a biotic factor, it does not conform to any such requirements. As a type of biotic climax it may be called a "pasturing-conditioned-climax" to distinguish it from other artificially controlled communities such as may be conditioned by mowing, cultivation, burning, flooding or other agency.

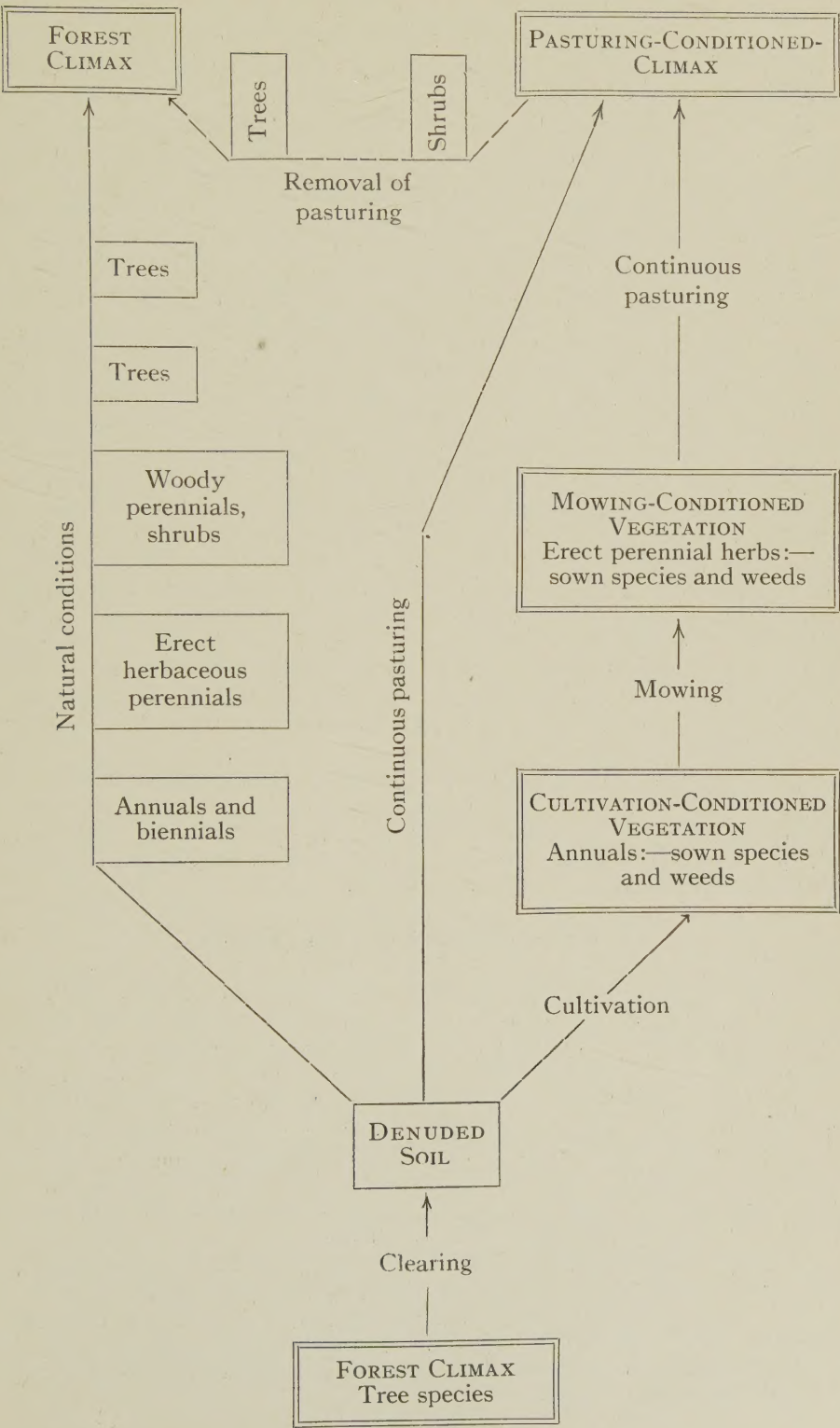


FIGURE 1. Secondary successions subsequent to clearing.

SUCCESSION SUBSEQUENT TO CLEARING

Most of the vegetation in settled areas of Eastern Canada has developed after the destruction of the forest climax in clearing of the land, and has come to its present status through the stages of a "secondary" succession. Under natural conditions the stages will be different in sequence and character from those of the primary succession but will culminate eventually in the same climax. When conditioned by continual grazing or by various cultural treatments, the succession is deflexed and proceeds through still other sequences. Starting with denuded soil on the newly cleared land, the probable stages in such naturally and artificially conditioned secondary successions may be briefly outlined with reference to Figure 1.

Invasion by annuals and biennials, especially those species which are most mobile, quickly ensues. Herbaceous perennials next come in and dominate the sward in the short interval while woody perennials are becoming established. The area now covered with shrubs and trees passes through several woodland types until the climax forest species are regained.

The usual objective in clearing, however, is to convert the land to agricultural purposes with cultivation and planting of crops. As long as tillage is an annual undertaking the vegetation on the land will not proceed beyond the association of the sown species, whether it be a grain, fodder or vegetable crop, with its concomitant and characteristic weeds. Farming practice involving a rotation does not allow the cultivation-conditioned vegetation to persist long, since land is usually sown down with a meadow mixture of perennial grasses and legumes. After harvesting hay from this mowing-conditioned vegetation for a few years, the stock are turned on and the typical hay species yield to the superior adaptability of their pasture-land counterparts.

The pasturing-conditioned-climax generally arises by this course in Eastern Canada but may be formed by a direct succession from denuded soil if stock are kept continually on the land after clearing. The vegetation, resulting, whether directly or through a series of intermediate stages determined by management practices, is similar.

PASTURING-CONDITIONED VEGETATION

Character

In the Eastern Townships vegetation in the pasture-conditioned stage has, until recently, been stinted of systematic ecological investigation. From our immature and incomplete knowledge, generalization as to its nature must be advanced with caution. Besides its distinctive origin and development, another tacit characteristic marks out this formation as a floral entity. The vegetation is typified by plants (1) of herbaceous nature, (2) of perennial duration, (3) reproducing by vegetative means, (4) of a growth-form adapted to repeated and close defoliation, and (5) introduced from foreign regions. A list of the plants found in permanent pastures in the area studied is given in Table 1.

On typical permanent grazing land the species, as has been mentioned, are all herbs, lacking in woody or secondary aerial growth and dying down to the ground at the approach of winter. Shrubby plants such as *Spiraea*, *Crataegus*, *Rubus*, *Betula*, etc., spring up only in positions where grazing has been prevented or on land that has been understocked or withheld from grazing for some time.

TABLE 1.—LIST OF PLANTS IN PERMANENT PASTURES, COWANSVILLE AREA, QUEBEC.

Botanical Name	Common Name	Abundance	Origin	Duration	Propagation
Legumes					
<i>Trifolium agrarium</i> L.	Hop clover	F	I	B	Se
<i>T. pratense</i> L.	Red clover	S	I	P	Se
<i>T. repens</i> L.	White clover	VC	I	P	St
<i>Vicia Cracca</i> L.	Blue vetch	R	I	P	Se
Useful Grasses					
<i>Agropyron repens</i> (L.) Beauv.	Couch-grass	S	I	P	Rh
<i>Agrostis solonifera</i> L., var. <i>major</i> (Gaud.) Farw.	Red-top	VC	I	P	Rh
<i>A. solonifera</i> L., var. <i>compacta</i> Hartm.	Creeping bent-grass	S	I	P	St
<i>Agrostis tenuis</i> Sibth.	Brown-top	R	I	P	Rh
<i>Dactylis glomerata</i> L.	Orchard grass	R	I	P	Se
<i>Festuca elatior</i> L.	Meadow fescue	F	I	P	Se
<i>F. rubra</i> L.	Red fescue	VC	?	P	Rh
<i>Glyceria striata</i> (Lam.) Hitchc.	Nerved manna-grass	F	N	P	Rh
<i>Phleum pratense</i> L.	Timothy	C	I	P	Se
<i>Poa annua</i> L.	Annual blue-grass	R	I	A	Se
<i>P. compressa</i> L.	Canada blue-grass	F	I	P	Rh
<i>P. pratensis</i> L.	Kentucky blue-grass	VC	I	P	Rh
<i>P. palustris</i> L.	Fowl blue-grass	R	N	P	Rh
Miscellaneous Plants					
A. Major Species					
<i>Achillea Millefolium</i> L.	Yarrow	C	?	P	Rh
<i>Antennaria neglecta</i> Greene	Antennaria	F	N	P	St, Ro
<i>Carex</i> , 10 species	Sedges	F, R	N	P	Rh
<i>Cerastium vulgatum</i> L.	Mouse-ear chickweed	C	I	P	Se, St
<i>Chrysanthemum Leucanthemum</i> L.	Ox-eye daisy	C	I	P	Se, Ro
<i>Danthonia spicata</i> (L.) Beauv.	Poverty-grass	C	N	P	Se
<i>Digitaria Ischaemum</i> (Schr.) Muhl.	Small crab-grass	F	I	A	Se
<i>Hieracium aurantiacum</i> L.	Orange hawkweed	VC	I	P	St, Ro
<i>H. florentinum</i> All.	Yellow hawkweed	F	I	P	St, Ro
<i>Hydrocotyle americana</i> L.	Marsh pennywort	F	N	P	St
<i>Juncus</i> (<i>J. macer</i> + and 3 minor spp.)	Rushes	C, R	N	P	Rh, Se
<i>Oxalis europaea</i> Jord.	Yellow wood-sorrel	C	I	P	Se, St
<i>Panicum lanuginosum</i> Ell.	Woolly panic-grass	C	N	P	Se, Ro
<i>Plantago major</i> L.	Common plantain	C	?	P	Se, Ro
<i>Prunella vulgaris</i> L.	Heal-all	VC	N	P	St
<i>Ranunculus acris</i> L.	Tall buttercup	C	I	P	Se, Ro
<i>Rumex Acetosella</i> L.	Sheep's sorrel	F	I	P	Se, Rh
<i>Stellaria graminea</i> L.	Stitchwort	C	I	P	St
<i>Taraxacum officinale</i> Weber	Common dandelion	VC	I	P	Se, Rt
<i>Veronica serpyllifolia</i> L.	Thyme-leaf speedwell	C	I	P	St
<i>Viola conspersa</i> Reich.	Dog violet	S	N	P	Se, Rh
<i>V. pallens</i> (Banks) Brainerd	White violet	C	N	P	Se, St
B. Minor Species					
<i>Acalypha virginica</i> L.	Three-seeded mercury	R	I	A	Se
<i>Ambrosia artemisiifolia</i> L.	Ragweed	R	I	A	Se
<i>Carum Carvi</i> L.	Caraway	S	I	P	Ro, Rt
<i>Cirsium arvense</i> (L.) Scop.	Canada thistle	F	I	P	Rh
<i>C. lanceolatum</i> (L.) Hill	Bull thistle	R	I	B	Ro
<i>Cyperus diandrus</i> Torr.	Low cyperus	F	N	A	Se
<i>Echinochloa crusgalli</i> (L.) Beauv.	Barnyard grass	R	I	A	Se
<i>Equisetum arvense</i> L.	Common horsetail	R	N	P	Rh
<i>Erigeron annuus</i> (L.) Pers.	Daisy fleabane	R	N	A	Se, Ro
<i>E. philadelphicus</i> L.	Philadelphia fleabane	S	N	P	St, Ro
<i>E. ramosus</i> (Walt.) BSP.	Daisy fleabane	S	N	A	Se, Ro
<i>Fragaria virginiana</i> Duchesne	Wild strawberry	F	N	P	St
<i>Galium Claytoni</i> Michx.	Clayton's bedstraw	R	N	P	St
<i>G. palustre</i> L.	Marsh bedstraw	R	N	P	St
<i>Geum canadense</i> Jacq.	Canada avens	R	N	P	Se
<i>G. strictum</i> Ait.	Yellow avens	R	N	P	Se
<i>Gnaphalium uliginosum</i> L.	Low cudweed	R	N	A	Se
<i>Hedeoma pulegioides</i> (L.) Pers.	American pennyroyal	S	N	A	Se

TABLE 1.—LIST OF PLANTS IN PERMANENT PASTURES, COWANSVILLE AREA, QUEBEC—*Con.*

Botanical Name	Common Name	Abundance	Origin	Duration	Propagation
<i>Hypericum canadense</i> L.	Canada St. Johnswort	R	N	A	Se
<i>H. mutilum</i> L.	Dwarf St. Johnswort	S	N	A	Se
<i>H. perforatum</i> L.	Common St. Johnswort	R	I	P	St
<i>Leontodon autumnalis</i> L.	Fall dandelion	F	I	P	Ro, Rt
<i>Linum catharticum</i> L.	Dwarf flax	S	I	A	Se
<i>Lobelia inflata</i> L.	Indian tobacco	S	N	A	Se, Ro
<i>Lycopus americanus</i> Muhl.	Cut-leaved bugleweed	R	N	P	Rh
<i>L. uniflorus</i> Michx.	Northern bugleweed	F	N	P	Rh
<i>Oenothera perennis</i> L.	Sundrops	F	N	P	St, Ro
<i>Plantago lanceolata</i> L.	English plantain	F	I	P	Se, Ro
<i>Polygonum Hydropiper</i> L.	Common smartweed	R	I	A	Se
<i>Potentilla norvegica</i> L.	Rough cinquefoil	S	?	?	Se
<i>P. simplex</i> Michx.	Five-finger	F	N	P	St
<i>Rudbeckia hirta</i> L.	Black-eyed Susan	R	I	?	Se, Ro
<i>Scirpus atrovirens</i> Muhl.	Bulrush	F	N	P	Rh
<i>S. cyperinus</i> (L.) Kunth.	Wool-grass	R	N	P	Rh
<i>Senecio aureus</i> L.	Golden ragwort	R	N	P	Rh, Ro
<i>Setaria lutescens</i> (Weigel) Hubb.	Yellow bristle-grass	R	I	A	Se
<i>Sisyrinchium angustifolium</i> Mill.	Blue-eyed-grass	F	N	P	Rh
<i>Solidago canadensis</i> L.	Canada goldenrod	R	N	P	?
<i>S. graminifolia</i> (L.) Salisb.	Narrow-leaf goldenrod	R	N	P	?
<i>S. nemoralis</i> Ait.	Wood goldenrod	F	N	P	Ro
<i>S. rugosa</i> Hill.	Rough goldenrod	R	N	P	?
<i>Sonchus arvensis</i> L.	Perennial sow-thistle	R	I	P	Rh, Ro
<i>S. asper</i> (L.) Hill	Spiny sow-thistle	R	I	A	Se
<i>S. oleraceus</i> L.	Annual sow-thistle	R	I	A	Se
<i>Spiraea tomentosa</i> L.	Hardhack	S	N	P	Rh
<i>Sporobolus neglectus</i> Nash	Annual drop-seed	S	N	A	Se
<i>Veronica officinalis</i> L.	Common speedwell	S	I	P	St

Abundance (descending degrees): VC—very common; C—common; F—frequent; S—scarce; R—rare
Origin: N—native to NE North America; I—immigrant, introduced from distant region.

Duration: A—annual; B—biennial; P—perennial.

Propagation (chief method of spread or persistence under grazing conditions): Se—seed; St—stolon; Rh—rhizome; Ro—rosette; Rt—root.

NOTE.—This list is not complete for all species contributing to the pasture flora of this district and includes only those plants of open and well-drained land which are likely to be grazed by the stock. Plants among stones and shrubbery or otherwise inaccessible to the cattle or in places unsuitable for quadrat placement are not listed.

Pasture plants are, in the main, long-lived and hardy perennials. Annuals are scarce or rare, only two species, *Digitaria Ischaemum* and *Cyperus diandrus*, figuring sporadically in the seasonal flora. These bear inflorescences close to the ground, mature rapidly, and drop their seeds, which remain in surface soil to carry the plant over winter. Perennials, on the other hand, depend on various vegetative structures for perennation and spread. Rhizomes, spreading out underground and coming to the surface at some distance from the parent plant, are very characteristic. These are typically of stem rather than root structure and are possessed mainly by desirable pasture grasses such as *Poa pratensis*, *Agrostis stolonifera* var. *major*, *Festuca rubra* and *Agropyron repens*. Stolons, long prostrate surface runners, radiating from the crown of the plant and rooting at the nodes, are prevalent among successful forbs³ such as *Trifolium repens*, *Hieracium aurantiacum*, *Cerastium vulgatum*, *Veronica serpyllifolia* and *Viola pallens*. Rosette offsets formed by division of the tap-root, lateral

³ *Forbs* is a term used to designate "herbaceous plants other than grasses, sedges and rushes." They are mainly broad-leaved and dicotyledonous species.

budding of the caudex and geniculate stems or from basal cleistogamous seeds are other means of propagation and are of great survival value to such plants as *Taraxacum officinale*, *Antennaria neglecta*, *Chrysanthemum Leucanthemum* and *Danthonia spicata*.

Pasture plants, in virtue of their low and spreading habit, are able to keep their growing tips out of reach of the grazing animal. Extermination would be imminent if they were erect or upright. Unexposed growth points appear to be a salient characteristic of plants which endure the severe treatment of continuous close defoliation received in permanent pastures. Gramineous species, all exhibiting intercalary rather than acrogenous growth, are particularly well adapted to such conditions. Of the seventeen grasses found, eight contribute to the herbage as much as or more than all the forbs.

Nearly all the common grasses are introduced from foreign countries. *Danthonia spicata*, of very low forage value, and *Glyceria striata*, reported as containing hydrocyanic acid (1), are natives. The origin of *Festuca rubra*, which becomes locally dominant, is doubtful. The important forbs, *Trifolium repens*, *Cerastium vulgatum*, *Chrysanthemum Leucanthemum*, *Hieracium* spp., *Ranunculus acris*, *Taraxacum officinale*, etc., are naturalized also. The origin of *Achillea Millefolium*, *Plantago major* and *Prunella vulgaris* has been subject to discussion (38). The majority of the aforementioned forbs are condemned as "weeds" when growing on cultivated land, but their status as such is questionable in pastures (23).

Stabilization and Type

Fifteen to twenty years are all that are required to effect stability between the vegetation and the grazing animal. The equilibrium, however, is not absolute in the strict sense of inertness, for as in all formations, forest or pasture, individuals run their life's cycle, pass out of the picture, and are supplanted by the more youthful individuals of the same species. Constancy, too, is only such as is to be expected within the range of intra-seasonal variation and variations caused by aberrant meteorological conditions. "Quasi-stability" might be a term of greater propriety to describe the situation, since, besides these variations, changes in the floral type have been shown by some (7) to attend changes in the depletion level of soil fertility brought about over long periods of time by continual cropping and removal of the product or by leaching and erosion. Differentiation of type from this cause is evolved with relative slowness. Fertility as determined by moisture relationships and the chance introduction of species has a more important bearing on type distribution.

Pasture types are generally classified according to characteristic gramineous species. There are blue-grass (*Poa pratensis*) pastures, red-top (*Agrostis stolonifera*) pastures, fescue (*Festuca rubra*) pastures, and poverty-grass (*Danthonia spicata*) pastures, depending on the species predominating. The separation is by no means sharp cut, since several (or all) species may occur, or more than one predominate, on a single area.

SUCCESSION ATTENDING AND SUBSEQUENT TO FERTILIZATION

Disturbing Factor and Processes

We have assumed that the pastures chosen for experimentation were in a state of relative stability as constantly controlled by the grazing cattle which, along with moisture, temperature and soil, are to be considered

as a factor in the environment. With the advent into this balanced community of a new factor—suddenly increased soil fertility due to applied fertilizers—equilibrium is upset. The disturbance and the resultant fluctuations are due to many causes, which may be expressed in the three major functions of the plant. First there is the *response* of the individuals already present. Response may be manifested as the more rapid and more extensive growth of both root and shoot, the production of more succulent and more nutritious herbage, etc. Response furthermore is a matter of degree and always relative to species (30), so we may expect greater change in some species than in others. This is followed by the *reaction* of the plant on the environment as exhibited in the encouragement of grazing with coincident increase in amount of trampling and manure, the addition of some soil nutrients and removal of others, the shading of the soil surface with its effect on evaporation and temperature, the effect on soil micro-organisms, the direct effect on other plants due to competition, etc. These changes (in its environment) act back on the plant. *Coaction*, as it has been called, is now already under way, showing up as an indirect effect of the original response of individual plants and species on the other individuals and species. Coaction, like response, is also specific, species acting in differential manner and degree. *Competition*, then, is the consequence of reaction in part (direct) but is also involved in coaction (indirect). *Experimental Areas and Methods*

Location of pastures:—The areas reported on are situated within a radius of fifteen miles of the town of Cowansville, Quebec. These permanent pastures were selected as typically representative of the Brown Forest Soil Zone of the province, the distribution and nature of which has already been described (22, 37).

A series of plots were laid out in 1931 to test the effect of surface-applied fertilizer. These plots were known as Series I and were situated on five different farms. New areas were brought under observation in subsequent years, when seven pastures of Series II, five pastures of Series III, and three pastures of Series IV were treated in 1932, 1933 and 1934 respectively.

Only three of the pastures in Series I were analysed to determine the sequential changes here described. The plots were 1 × 2 rods in size and received surface treatments with the elements of fertility in April, 1931, according to the following formulae:—CaNPK, NPK, CaPK, PK, Ca, Nil, CaP, P, CaK, K. The arrangement of the 10 plots and the amounts and kinds of fertilizers applied have been described by other investigators (26, 37).

Method of botanical analysis:—Qualitative and quantitative studies of pasture vegetation elsewhere have involved the use of various instruments and quadrats differing in size (3, 18, 27), shape (6), number (21), type (17, 20), and basis of analysis (10, 11, 24, 25).

The method employed in the permanent pastures in the Cowansville area was based on an ocular estimation of the percentage ground covered by the plants in quadrats. This method was found to be well adapted to the nature of the vegetation and to the purpose for which it was required that of recording the species present, their relative proportions, and changes in their degree of prevalence. Methods of analysis requiring tiller or

plant counts, hand separation, charting or lifting of turfs would have been impracticable in the close and interwoven sod.

The grid-quadrat consisted of a wooden frame with fine wires stretched across it and dividing it into 25 equal sub-squares. On Series I a frame 20×20 cm. was used, but on plots laid out later a larger frame, 50×50 cm., was used to some advantage. Four positions were selected on each plot, care being taken to avoid stones, droppings, or areas unrepresentative of the pasture as a whole. The positions were marked with a permanent stake, driven in the ground at the upper left-hand corner of the frame, so that the readings could be made on exactly the same area at subsequent dates.

The percentage ground covered was obtained by estimating the proportion of the area of each sub-square occupied by each individual species. Space not covered by any plant was recorded as *bare ground*. Each square was given the value of 10, and the proportions allotted were in units of this amount. Half-units and quarter-units were also used for species present in lesser degrees. The total for the 25 sub-squares was 250 and for the 4 quadrats on the plot 1,000, from which percentages were easily calculated.

All analyses were made under light conditions as uniform as could be obtained by shading the quadrat area from direct sunlight. An attempt was made to make the readings at the same date each year to eliminate seasonal variations. The dates of quadratting were as follows:—Sept. 7 to 28, 1931; Sept. 13 to 22, 1932; Sept. 12 to 16, 1933; Sept. 13 to 19, 1934.

Changes Initiated by Disturbing Factor

In order to study the actual changes that might take place in the stabilized vegetation of old pastures due to the application of fertilizer, three experimental areas in Series I were selected. These were on farms situated in different directions within ten miles of the town of Cowansville. The estimates on quadrat areas obtained by the method outlined above were averaged for the three pastures and are presented in Table 2. In these data for each of eight of the differently treated plots over the period of four years, 1931 to 1934, each figure represents the average of 12 quadrat areas, 4 at each of the 3 farms. The figures in heavy face type, the percentage ground covered by legumes (all *Trifolium repens*), total useful grasses, total miscellaneous plants, and bare ground, are plotted in graph form in Figure 2 and illustrate the sequence of changes attending and subsequent to treatment.

In surveying these data and charts, one should keep in mind two points relevant to the experiment. First, limestone and mineral fertilizers were applied but once, the former in October, 1930, and the latter in April, 1931. Gradual depletion of the added elements and certain of those of natural fertility has taken place in the four years, no replenishment being attempted. Second, the changes that have occurred have not been due solely to the direct effect of fertilizer but also to the coactions mentioned above. Among these, perhaps the most important is the increased intensity of grazing induced by the more palatable herbage on fertilized plots. The proximity of the untreated (Nil) plot has brought about closer grazing on it also. Changes in the herbage composition of this plot may therefore

TABLE 2.—PERCENTAGE GROUND COVERED BY SPECIES AND GROUPS OF PLANTS OVER A PERIOD OF FOUR YEARS SUBSEQUENT TO FERTILIZATION. EACH FIGURE REPRESENTS THE AVERAGE OF 12 QUADRATS, 4 ON A PLOT AT EACH OF THE 3 PASTURES OF SERIES I.

	CaNPK				NPK				CaPK				PK			
	1931	1932	1933	1934	1931	1932	1933	1934	1931	1932	1933	1934	1931	1932	1933	1934
Legumes																
<i>Trifolium repens</i> ¹	54.2	34.4	19.2	7.2	42.9	32.2	16.1	8.6	49.1	33.6	19.5	9.2	48.7	34.9	16.1	9.8
Useful Grasses																
<i>Agrostis stolonifera</i>	24.3	34.0	32.3	37.3	25.3	32.5	33.1	29.4	18.1	29.2	26.6	30.8	17.6	26.3	33.2	25.7
<i>Phleum pratense</i>	1.5	2.9	7.2	9.1	0.4	0.8	2.1	2.1	1.9	4.7	7.7	7.3	0.6	1.4	2.4	3.7
<i>Poa pratensis</i> ²	4.7	9.5	18.0	19.7	3.8	9.3	18.1	23.0	1.8	5.0	9.3	8.9	4.8	7.5	15.2	20.9
Other grasses ³	0.0	0.1	0.2	0.5	1.6	1.5	2.6	1.7	1.2	2.1	4.7	4.0	0.7	0.8	1.4	0.2
Total Useful Grasses	30.5	46.5	57.7	66.6	31.1	44.1	55.9	56.2	23.0	41.0	48.3	51.0	23.7	46.0	52.2	50.5
Miscellaneous Plants																
<i>Cerastium vulgatum</i>	1.2	2.1	1.5	0.8	1.4	1.3	1.2	0.5	1.6	1.7	1.8	1.7	1.1	0.9	1.4	0.3
<i>Chrysanthemum Leucanthemum</i>	0.1	0.0	0.3	0.0	0.9	1.0	0.5	1.0	0.4	0.6	0.6	1.2	0.5	0.1	0.4	1.5
<i>Hieracium aurantiacum</i>	0.3	0.0	0.0	0.2	0.9	1.6	1.3	1.9	1.8	1.2	1.2	1.1	1.4	2.2	1.6	2.4
<i>Plantago major</i>	1.3	0.8	0.8	0.6	0.7	1.0	0.8	1.0	1.8	0.5	0.6	0.6	1.0	2.1	0.8	0.9
<i>Prunella vulgaris</i>	0.7	0.7	0.3	0.1	0.8	0.2	0.3	0.5	0.7	0.7	1.3	0.5	1.2	0.9	0.9	1.0
<i>Ranunculus acris</i>	0.4	0.4	0.6	1.1	0.8	1.1	0.5	0.9	1.0	1.2	1.0	2.7	0.7	0.5	0.3	1.2
<i>Taraxacum officinale</i>	1.5	2.4	2.6	4.9	2.8	1.9	2.4	5.1	2.6	1.1	2.2	2.7	1.5	1.8	1.8	3.6
Other plants ⁴	3.4	2.9	3.3	3.3	3.7	3.8	3.0	4.3	4.9	3.7	3.7	4.1	4.2	6.1	4.9	5.7
Total Miscellaneous Plants	8.9	9.3	9.4	11.0	12.0	11.9	10.0	15.2	14.8	10.9	12.4	14.6	11.6	14.6	12.1	16.6
Bare Ground ⁵	6.4	9.8	13.7	15.2	14.0	11.8	18.0	20.0	13.1	14.5	19.8	25.2	16.5	14.5	19.6	23.1

	Ca				Nil				CaP				P			
	1931	1932	1933	1934	1931	1932	1933	1934	1931	1932	1933	1934	1931	1932	1933	1934
Legumes																
<i>Trifolium repens</i> ¹	21.7	21.9	13.5	8.4			8.6	5.2			16.6	12.8	32.1	26.6	20.4	19.7
Useful Grasses																
<i>Agrostis stolonifera</i>	29.2	35.8	29.6	27.0	19.8	27.8	27.6	22.4	26.4	36.7	32.1	30.9	20.7	30.4	26.1	20.9
<i>Phleum pratense</i>	1.5	5.9	5.5	12.0	0.7	2.1	3.0	5.4	0.8	3.5	3.8	5.0	0.8	2.8	2.3	4.0
<i>Poa pratensis</i> ²	2.1	4.3	8.4	10.5	4.2	5.7	8.0	9.1	1.3	4.0	10.3	8.8	3.7	6.9	9.6	4.7
Other grasses ³	0.4	1.0	1.1	0.3	4.1	2.5	2.9	1.6	0.2	0.5	0.1	0.7	1.7	1.1	0.7	0.9
Total Useful Grasses	33.2	47.0	44.6	49.8	28.8	38.1	41.5	38.6	28.7	44.7	46.3	45.4	26.9	41.2	38.7	30.5
Miscellaneous Plants																
<i>Cerastium vulgatum</i>	1.6	0.5	1.2	0.9	0.9	0.5	1.1	0.3	0.8	0.3	1.0	1.4	1.3	0.9	1.0	0.3
<i>Chrysanthemum Leucanthemum</i>	1.5	1.6	1.3	1.4	2.7	2.4	1.6	1.9	0.6	0.3	0.7	0.3	1.4	1.7	0.8	1.3
<i>Hieracium aurantiacum</i>	2.8	2.5	1.9	2.0	2.9	3.1	4.5	6.9	1.3	0.7	0.8	0.2	2.6	2.8	2.3	4.5
<i>Plantago major</i>	1.8	1.0	1.5	1.4	1.4	0.8	0.9	3.0	2.8	1.8	0.8	2.1	2.4	1.5	1.2	1.3
<i>Prunella vulgaris</i>	2.6	2.6	2.0	1.5	1.5	2.5	1.9	1.4	1.5	1.0	1.7	0.8	2.7	2.7	2.8	0.6
<i>Ranunculus acris</i>	1.5	1.5	0.8	1.1	1.2	0.9	0.9	0.9	1.4	1.1	0.6	1.0	1.2	1.0	0.8	0.7
<i>Taraxacum officinale</i>	2.3	2.1	3.2	3.0	3.2	4.5	3.5	5.2	1.8	1.0	2.2	3.7	2.5	1.6	1.9	2.6
Other plants ⁴	10.9	7.7	4.2	7.4	10.9	11.8	11.0	10.9	7.4	6.0	5.1	11.6	9.0	8.6	8.4	21.2
Total Miscellaneous Plants	25.0	19.5	16.1	18.7	24.7	26.5	25.4	30.5	17.6	12.2	12.9	21.1	23.1	20.8	19.2	32.4
Bare Ground ⁵	20.2	11.6	25.8	23.1	30.2	21.2	24.5	25.8	11.0	9.1	24.2	20.7	17.9	12.0	21.7	17.4

¹ The only legume on these pastures.

² Includes small amounts of *P. compressa*.

³ Composed of *Festuca rubra*, *Glyceria striata*, *Festuca elatior*, *Agropyron repens*.

⁴ Composed of *Juncus* spp., *Carex* spp., *Achillea Millefolium*, *Lycopus* spp., *Panicum lanuginosum*, *Viola* spp., *Danthonia spicata*, *Oxalis europaea*, *Fragaria virginiana*, *Antennaria neglecta*, *Stellaria graminea*, *Cirsium* spp., *Potentilla simplex*, *P. norvegica*, *Sisyrinchium angustifolium*, *Lobelia inflata*, *Scitago* spp., *Kumex Acetosella*, *Hedeoma pulegioides*, *Oenothera perennis*, *Cyperus diandrus*, *Hydracolea americana*, *Hypericum* spp., *Digitaria Ischacium*, *Hieracium florentinum*, *Erigeron* spp., *Sonchus* spp., *Veronica serpyllifolia*, and other species.

⁵ Composed of mosses lichens, stones and bare soil.

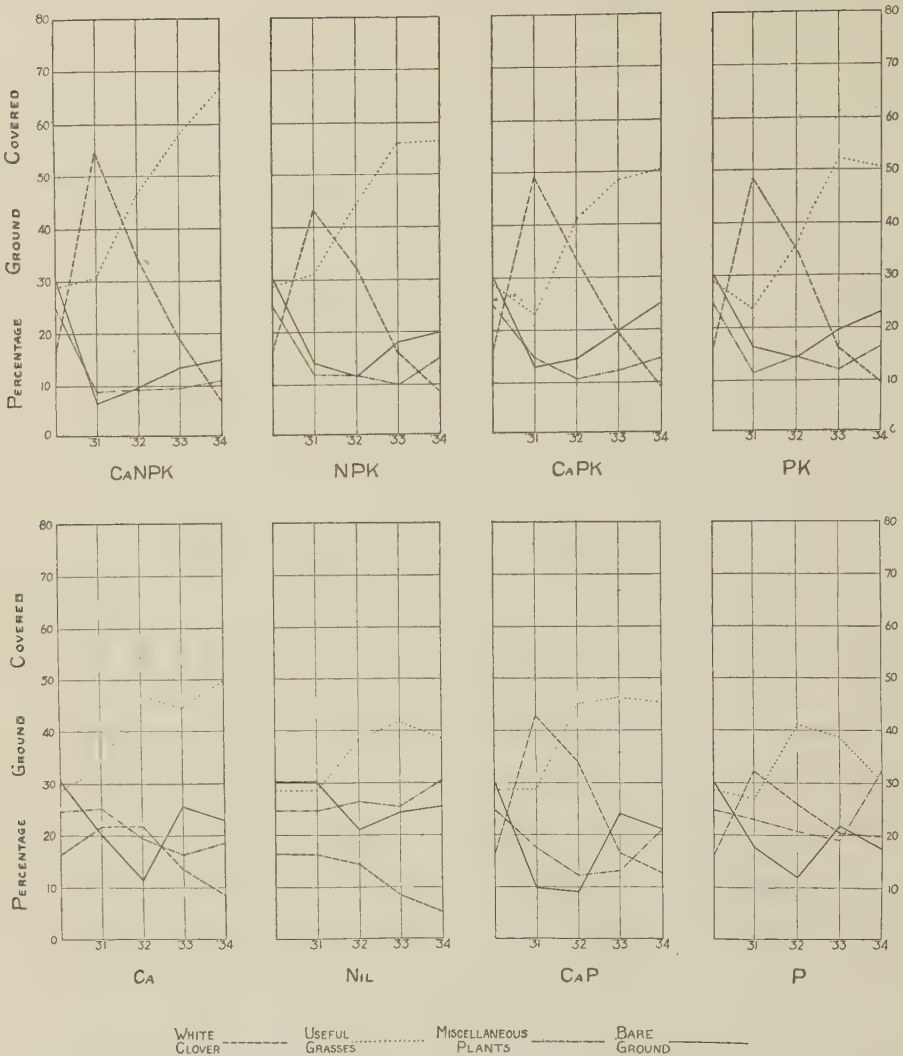


FIGURE 2. Graphs to show the variations in the percentage ground covered by groups of plants and bare ground on the experimental plots at three pastures in the Cowansville area over the four year period, 1931 to 1934, inclusive. The percentage on the nil plot in the first year is the starting point in each graph.

be ascribed to increased grazing of the turf and also to differences in seasonal conditions at times of quadratting. Since the latter would affect all plots, this change and part of that due to the former cause may be eliminated by expressing all readings on a relative basis (see Table 3).

Changes in Specific Composition of Sward

Surveying the general changes from year to year, we find the most striking to be those concerning the leguminous constituent of the sward. *Trifolium repens*, the only legume present, increased greatly on all superphosphate (P) plots in the year of application, sometimes becoming as much as three times as abundant as on the untreated. The limestone

TABLE 3.—RELATIVE GROUND COVERED BY GROUPS OF PLANTS OVER A PERIOD OF FOUR YEARS SUBSEQUENT TO FERTILIZATION. EACH FIGURE IS CALCULATED FROM THE AVERAGE OF 12 QUADRATS, 4 ON A PLOT AT EACH OF THE 3 PASTURES OF SERIES I, BY EXPRESSING THE PERCENTAGES IN TABLE 2 IN TERMS RELATIVE TO THE NIL PLOT EACH YEAR.

	CaNPK				NPK				CaPK				PK			
	1931	1932	1933	1934	1931	1932	1933	1934	1931	1932	1933	1934	1931	1932	1933	1934
Legumes (<i>T. repens</i>)	332	241	224	138	263	227	189	164	300	236	228	176	295	245	188	179
Total useful grasses	106	122	139	173	108	115	135	146	80	107	116	133	82	94	126	131
Total miscellaneous plants	36	35	37	36	49	45	39	50	60	41	49	48	47	55	48	54
Bare ground	21	46	56	59	47	56	74	78	44	68	81	98	55	69	80	90

	Ca				Nil				CaP				P			
	1931	1932	1933	1934	1931	1932	1933	1934	1931	1932	1933	1934	1931	1932	1933	1934
Legumes (<i>T. repens</i>)	133	154	158	160	100	100	100	100	262	239	194	245	197	183	238	376
Total useful grasses	115	123	107	129	100	100	100	100	100	117	112	118	94	108	93	80
Total miscellaneous plants	101	74	63	62	100	100	100	100	31	46	51	69	94	79	75	106
Bare ground	67	55	105	90	100	100	100	100	36	43	99	80	59	56	89	68

(Ca) by itself stimulated the clover only slightly, but when applied along with the other elements the increases were more marked. It was found that white clover responds immediately and proves itself capable of rapid and extensive proliferation, readily spreading itself out to occupy all bare spaces in the sod or between other plants. Bare ground takes a decided drop on all plots. Nearly all the forbs (other than *Trifolium repens* itself), especially *Hieracium aurantiacum*, *Prunella vulgaris*, *Ranunculus acris*, *Chrysanthemum Leucanthemum*, and undesirable narrow-leaved species such as belong to *Juncus* and *Carex*, and *Panicum lanuginosum* go down, and their space too is taken by *Trifolium repens*. It does not appear correct to assume that these plants are forced down to smaller areas due to invasion pressure, since *Trifolium repens* as an aggressor and invader is not very potent as shown by its behaviour in subsequent years, but due more probably to their inability to withstand the almost complete defoliation by grazing.

The useful grasses, as a whole, remain more or less constant in the first year. In the second, however, their increase is sharply marked. The increase continues into the third year, when they become the most abundant constituents of the sward. The white clover declines, or better, is forced to decline due to the demands exerted on its territory by the slower growing, but stronger growing, grasses. During the rise of the grasses to prominence, the miscellaneous plants and bare ground remain at a low level or tend to increase only after three years.

The trends exhibited by some of the individual species of useful grasses are also shown in the figures in Table 2. The tendency is towards an increase in ground cover in all species, as might be expected. *Agrostis stolonifera*, the most abundant species, shows irregular changes over the

four years and on all plots. When expressed in terms relative to the Nil plot, they tend to smooth out, indicating that they are probably due to seasonal conditions existing at time of quadratting. *Phleum pratense*, although present in small amount, makes relatively large increases after the first year on the Ca plots. The case of *Poa pratensis* is quite striking on the CaNPK, NPK and PK plots, where increases are five-fold in four years. On the other treatments the change relative to Nil is slight. The few other species of grasses drop sharply in the first year and remain in small quantity except on CaPK, where there happens to be a high percentage of *Festuca rubra* on this plot at one of the pastures.

Significant Changes in Major Groups

The changes in ground covered from year to year were tested by the Standard Error method and are summarized in Table 4. The percentages

TABLE 4.—CHANGE IN PERCENTAGE GROUND COVERED BY THE GROUPS OF PLANTS AND BARE GROUND, WITH STANDARD ERRORS CALCULATED.

Treat- ment	In 1931*	1931 to 1932	1932 to 1933	1933 to 1934	1931 to 1933	1932 to 1934	1931 to 1934
A. White Clover (<i>Trifolium repens</i>)							
CaNPK	+37.9±6.5	-19.8±7.5	-15.2±4.6	-12.0±2.4	-35.0±6.7	-27.2±4.1	-47.0±6.4
NPK	+26.6±5.4	-10.7±6.3	-16.1±5.7	-7.5±4.3	-26.8±6.5	-23.6±3.9	-34.3±5.1
CaPK	+32.8±6.0	-15.5±6.9	-14.1±4.5	-10.3±2.5	-29.6±6.2	-24.4±4.1	-39.9±5.8
PK	+31.9±5.9	-13.3±6.9	-18.8±4.5	-6.3±2.2	-32.1±5.9	-25.1±4.2	-38.4±5.7
Ca	+5.4±3.2	+0.2±3.6	-8.4±3.0	-5.1±1.9	-8.2±3.0	-13.5±2.7	-13.3±2.7
Nil		-2.1±2.5	-5.6±1.9	-3.4±1.2	-7.7±2.2	-9.0±1.8	-11.1±2.0
CaP	+25.4±5.3	-8.7±6.4	-17.4±4.4	-3.8±2.4	-26.1±5.3	-21.2±4.2	-29.9±5.2
P	+15.8±4.2	-6.1±4.8	-5.6±3.9	-0.7±3.3	-11.7±4.4	-6.3±3.8	-12.4±4.4
B. Useful Grasses							
CaNPK	+1.7±2.9	+16.0±3.9	+11.2±5.2	+8.9±6.2	+27.2±4.6	+20.1±5.7	+36.1±5.2
NPK	+2.3±3.0	+13.0±3.8	+11.8±5.0	+0.3±5.6	+24.8±4.5	+12.1±5.0	+25.1±4.5
CaPK	-5.8±2.6	+18.0±3.3	+7.3±4.5	+2.7±5.0	+25.3±3.8	+10.0±4.6	+28.0±4.0
PK	-5.1±2.6	+12.3±3.0	+16.2±4.5	-1.7±5.2	+28.5±4.0	+14.5±4.4	+26.8±3.9
Ca	+4.4±3.1	+13.8±4.1	-2.6±4.6	+5.2±4.7	+11.4±3.9	+2.8±4.8	+16.6±4.2
Nil		+9.3±3.4	+3.4±4.0	-2.9±4.0	+12.7±3.6	+0.5±3.8	+9.8±3.4
CaP	-0.1±2.9	+16.0±3.8	+1.6±4.5	-0.9±4.6	+17.6±3.8	+0.7±4.5	+16.7±3.8
P	-1.9±2.8	+14.3±3.5	-2.5±4.0	-8.2±3.5	+11.8±3.3	-10.7±3.6	+3.6±2.9
C. Miscellaneous Plants							
CaNPK	-15.8±4.4	+0.4±2.2	+0.1±2.2	+1.6±2.4	+0.5±2.2	+1.7±2.4	+2.1±2.4
NPK	-12.7±4.6	-0.1±2.9	-1.9±2.6	+5.2±3.1	-2.1±2.7	+3.3±3.3	+3.3±3.3
CaPK	-9.9±4.9	-3.9±3.1	+1.5±3.4	+2.2±3.8	-2.5±3.8	+3.7±3.1	-0.2±3.5
PK	-13.1±4.6	+3.0±3.1	-2.5±3.2	+4.5±3.5	+0.5±2.8	+2.0±3.7	+5.0±3.4
Ca	+0.3±5.9	-5.5±5.3	-3.4±4.3	+2.6±4.2	-8.9±5.0	-0.8±4.6	-6.3±5.3
Nil		+1.8±6.1	-1.1±6.2	+5.1±6.7	+0.7±6.0	+4.0±6.8	+5.8±6.5
CaP	-7.1±5.1	-5.4±3.6	+0.7±3.0	+8.2±4.2	-4.7±3.7	+8.9±4.1	+3.5±4.6
P	-1.6±5.7	-2.3±5.3	-1.6±4.8	+13.2±4.8	-3.9±5.1	+11.6±4.9	+9.3±5.2
D. Bare Soil and Moss							
CaNPK	-23.8±1.5	+3.4±1.5	+3.9±2.2	+1.5±2.7	+7.3±2.0	+5.4±2.4	+8.8±2.2
NPK	-16.2±2.2	-2.2±2.6	+6.2±2.8	+2.0±3.5	+4.0±3.0	+8.2±3.0	+6.0±3.2
CaPK	-17.1±2.1	+1.4±2.6	+5.3±3.2	+5.4±4.2	+6.7±3.1	+10.7±3.8	+12.1±3.7
PK	-13.7±2.5	-2.0±2.9	+5.1±3.2	+3.5±4.0	+3.1±3.4	+8.6±3.6	+6.6±3.7
Ca	-10.0±2.9	-8.6±3.0	+14.2±3.7	-2.7±4.5	+5.6±4.3	+11.5±3.4	+2.9±4.0
Nil		-9.0±4.8	+3.3±4.2	+1.3±4.6	-5.7±5.1	+4.6±4.4	-4.4±5.2
CaP	-19.2±1.9	-1.9±1.8	+15.1±3.4	-3.5±4.2	+13.2±3.5	+11.8±1.6	+9.7±3.1
P	-12.3±2.6	-5.9±2.8	+9.7±3.2	-4.3±3.6	+3.8±3.7	+5.4±2.8	+0.5±3.2

*Relative to Nil the same year.

NOTE.—Figures in **heavy type** indicate changes sufficiently great to be significant as measured at the 0.05 point of probability.

in bold face type are those reaching the 5% point of significance as measured by the "t" test of Fisher (15).

Legumes vs. grasses.—The inverse relations between the ground covered by legumes and by grasses may be due to several conditions.

(1) The relative inherent property of the two kinds of plants for rapid proliferation is different. The habit of growth of *Trifolium repens* by surface stolons enables it to spread without any great obstruction. The grasses, however, are rhizomatous and are able to send out new shoots only through the soil. It is needless, therefore, to stress the point that, granted both these types benefit to the same extent by the increased fertility, the relative rate at which they respond can be quite different.

(2) The white clover, also on account of its vegetative habit, is able to send out roots which establish contact with and exploit the surface soil. Investigations already in progress (43) show that the half-inch of soil on the surface is the concentration zone for surface-applied phosphates. White clover, rather than the deeper-rooted grasses, is therefore in a more opportune position to utilize this supply.

(3) An increase in soil nitrates accompanies the increase of legumes, since these plants have the singular characteristic of association with symbiotic nitrifying micro-organisms. There is much evidence to indicate that grasses are relatively more efficient in their powers to utilize nitrogen (4, 16, 28, 40). The clovers, then, by building up an excess of nitrates in the soil, indirectly tend to modify their environment in such a manner as to make it relatively more ameliorative to grasses than to themselves. This, in a general way, is the essence of all plant succession.

It has sometimes been demonstrated that clover can be maintained at a high level in a pasture by proper management (19, 35). It is impossible to support such a contention from the data here presented but it is probable that such might have been the case had a constant level of fertility been maintained. The figures and graphs indicate that the fertilizer is becoming depleted in the fourth year, and the various constituents of the vegetation are approaching their pre-treatment proportions.

INTRA-SEASONAL VARIATIONS

Besides the successional changes taking place from year to year as just described, there are definite fluctuations in the abundance and kind of species in the pasture sward within the growing season. These are caused by the influence of (1) meteorological conditions, (2) inherent periodicity of species, (3) varying grazing intensity.

Meteorological Conditions

Change in the rate of growth of pasture herbage due to weather conditions is only too well known and has oftentimes proved a sad reality to the grazier. As early as 1888, Pennsylvania workers (2), measuring the yield of Kentucky blue-grass (*Poa pratensis*) pastures, found that production varied from month to month. Fagan and Jones (13) by clipping timothy (*Phleum pratense*) plots monthly found the variations in dry matter to follow the general trend from high in mid-May to low in mid-July to slightly higher in mid-August and constant from then on to October. By clipping the plots more often at weekly intervals, other English workers

	PASTURE B.				PASTURE C.				PASTURE D.				PASTURE E.		
	June 26	Aug. 17	Sept. 18		June 26	Aug. 17	Sept. 18		June 26	Aug. 17	Sept. 18		June 26	Aug. 17	Sept. 18
<i>Agrostis</i> spp.	32.5	30.3	37.9	- 2.2	+ 7.6	+15.4	29.6	21.5	26.3	- 8.1	+ 4.8	- 3.3			
<i>Carex</i> spp.	0.1	0.2	0.2				0.4	0.1	0.3						
<i>Cerastium vulgatum</i>	0.7	0.1	0.1				1.8	0.8	0.7	- 1.0	- 0.1	- 1.1			
<i>Chrysanthemum leucanthemum</i>	0.2	0.4	0.5				0.1	0.2	0.1						
<i>Cyperus diandrus</i>	0.0	0.0	1.8				0.0	0.0	0.0						
<i>Danthonia spicata</i>	0.5	0.2	0.3	+ 4.7	+ 2.3	+ 7.0	0.2	0.6	0.4	+10.7	+ 0.2	+10.9			
<i>Digitalis Ischaemum</i>	1.4	6.1	8.4				1.4	12.1	12.3	- 1.3	+ 0.4	- 0.9			
<i>Hieracium aurantiacum</i>	0.9	0.7	0.6	+ 0.2	- 1.3	- 1.1	3.9	2.6	3.0						
<i>Juncus macer</i>	1.6	1.8	0.5				0.3	0.2	0.2						
<i>Lobelia inflata</i>	0.0	0.0	0.1	- 0.1	- 0.6	- 0.7	1.1	1.2	0.7						
<i>Oxalis europaea</i>	1.0	0.9	0.3				0.0	0.0	0.0						
<i>Panicum lanuginosum</i>	0.5	0.6	0.2				0.7	0.7	0.7	- 0.4	+ 1.1	+ 0.7			
<i>Phleum pratense</i>	2.6	2.9	3.6				2.7	2.3	3.4						
<i>Plantago major</i>	7.9	7.1	7.2				2.2	3.4	3.3						
<i>Poa compressa</i>	1.6	1.4	1.4				0.8	1.6	1.0						
<i>Poa pratensis</i>	2.5	3.1	3.8				7.5	10.1	10.4	+ 2.6	+ 0.3	+ 2.9			
<i>Prunella vulgaris</i>	2.4	2.4	2.7	- 1.7	+ 0.2	- 1.5	3.9	4.2	5.4						
<i>Ranunculus acris</i>	3.8	2.1	2.3				2.1	2.0	1.3	- 0.1	- 0.7	- 0.8			
<i>Taraxacum officinale</i>	4.8	3.9	5.1				2.5	1.8	1.9						
<i>Trifolium repens</i>	12.7	8.7	10.4	- 4.0	+ 1.6	- 2.4	27.5	9.7	13.5	-17.8	+ 3.8	-14.0			
<i>Veronica serpyllifolia</i>	0.2	0.2	0.3				0.2	0.3	0.7						
<i>Viola</i> spp.	4.3	0.4	0.3	- 3.9	- 0.1	- 4.0	0.6	0.0	0.0						
Other species	1.8	1.7	1.8				1.2	1.4	1.2						
Bare soil + mosses	16.0	24.8	10.2	+ 8.8	-14.6	- 5.8	9.3	23.2	13.2	+13.9	-10.0	+ 3.9			

¹ Average of 4 quadrats.

² Figures in **heavy type** are significantly greater than the error as measured by the "t" test at the 5% point of probability.

(42) disclose similar large variations and also minor fluctuations dependent on moisture and temperature. In the period mid-June to September, when soil moisture is below the optimum, variations in yield correspond with variations in precipitation. The increases in yield, however, do not take place for a fortnight after the incidence of rainfall. In the early spring and late fall periods, when soil moisture is plentiful, rainfall ceases to be a determining factor, and variations in yield are correlated with changes in temperature. Shutt and his co-workers (32) at Ottawa found that fluctuations in each of two years were similar in that they were related to the precipitation in the preceeding week. Workers in Vermont (12) and in New Zealand (29) also stress the dependence of pasture productivity on the meteorological conditions.

Observations in the Eastern Townships pastures disclose irregular production following the trend of highest in June, lowest in July and August when growth slows up greatly, almost ceasing if drought is severe, and higher again in September. Changes are not as sharp on some pastures as on others on account of better soil-moisture conditions. Yield data from caged areas could not be used to demonstrate such fluctuations, since clippings were not taken at equal intervals. Botanical readings as made by ground-covered estimation methods give palpable indication of it.

For the most part, meteorological conditions affect most species in a similar manner, favourable periods bringing increased growth and increased ground covered by all. The decrease in the percentage area is taken up by the lessening of bare space and mosses. In unfavourable periods, as in late July and August, the large amount of bare ground recorded is due to the receding of most of the plants but especially of *Trifolium repens* and other broad-leaved plants on account of the greater shrivelling and drying of their foliage. The grasses and certain grass-like plants bearing narrow and erect leaves, maintain a more constant foliage cover throughout the season.

Inherent Periodicity

Seasonal productivity of pastures is affected as much as, or more by the plants' functional periodicity, than by meteorological conditions. Stapledon (34, 35) has pointed out that the season is, therefore, naturally divided into four periods, depending on the inherent characteristics of the plants for growth. The "awakening" period is from the time of first growth up to the heading stage. The "zenith" is a period of rapid and maximum growth and coincides with the heading and flowering stages. The "waning" period follows when growth slows up and remains at a low level until the "rapidly waning" period of when growth slows up further as the plants approach the dormant stage of no growth which endures over winter. Sometimes a "secondary zenith" is interposed previous to the rapidly waning period and corresponds to the aftermath growth of meadows, when inflorescences tend to produce again in many species. Stapledon shows, and is supported by certain American workers (39) who recognize similar charges, that the peaks in production take place regardless of rainfall, and the trend is the same even in abnormal years. The meteorological conditions, then, become secondary and are effective only in accentuating the periods, favourable conditions making the rush to

the zenith more pronounced, and unfavourable the drop in the waning period even greater.

All species, however, do not exhibit the same periodicity. Seasonal aspects are quite striking and familiar to all who observe the predominating plants of the pasture come into flower in their due course. A quotation from Sinclair (33) aptly states, "from the spring until the end of autumn, there is not a month but is the season of luxuriance of one or more grasses." Woodman *et al.* (42) give a resumé of the seasonal aspects of pastures as clovers, grasses and weeds come into prominence, showing that any one species rarely holds its position throughout the season. Fenton (14), from periodic quadrat readings, states that "the marked fluctuations in percentage ground covered by the leading species is an annual occurrence of considerable regularity."

Stapledon (34), working with pure species, shows that some have unimodal and some bimodal curves of production. Staples and Taylor (36) give similar results for species in South Africa. Blackman (5) gives curves indicating that the peak of seasonal productivity is reached, first by *Lolium perenne* in May, *Poa trivialis* in June, *Agrostis* spp. and *Trifolium repens* in July, then a secondary peak for *Lolium perenne* in August and September. Some agriculturists have taken this into account in attempting a mixture of species so selected and adjusted as to have species maturing at different periods in order to maintain uniform production during the course of the season.

It is doubtful how much success will be attained by this scheme for permanent pasture and other long duration swards in this country. In a climate such as ours, with seasons sharply divided into spring, summer, and fall by marked extremes in conditions of temperature and moisture, the species will soon be naturally selected to those fruiting at the season least favourable for vegetative growth. That this is actually the case is amply illustrated by records of the dates of flowering and fruiting of the chief species of natural pastures in the district studied. Most species tend to bloom from June 15 to July 15, the peak period of herbage production, and ripen seed in August when growth is restricted.

Experimental Results

Exact information as to the percentage of different species in the sward at periods during the season is very scarce for pastures in this country. A study was therefore undertaken in 1933 involving estimates on several pastures at approximately monthly intervals. Permanent quadrats, one-quarter square meter in area, located on the adjacent Nil and PK plots, were read, and the averages are recorded for two of the pastures in Table 5. It was impossible to group the data for all pastures since all readings could not be made at the same date and the floral composition differed considerably. Species which were fairly prevalent were treated statistically by Fisher's "z" test, standard errors were calculated, and if significant differences were indicated the changes from period to period were tested by the "t" test. The figures in bold type in the table are significantly larger than their error as measured at the 5% point.

From a survey of these data and from a study of individual quadrats it is apparent that a species rarely holds its same territory throughout the

season. The species may therefore be summarized into five categories, depending on their actions.

1. *Vernal species* that make their growth in the first half of the season and decrease, sometimes succumbing completely, in the period of drought in August and make little or no renewed growth in the fall are *Cerastium vulgatum*, *Viola* spp., *Juncus macer* and *Oxalis europaea*. These plants flower early and finish fruiting in mid-summer, new plants arising readily from seeds in the soil.

2. *Drought dormant species* include some of the major plants of the pasture. *Trifolium repens*, *Poa pretensis*, *Veronica serpyllifolia* and *Taraxacum officinale* allow their leaves to wither and dry up during the dry spell, retaining life in the stolons, underground rhizomes or roots, which put forth new foliage in the fall when moisture returns. *Phleum pratense* and *Agrostis stolonifera* carry themselves through drought in this way also.

3. *Aestival species* are very few. *Linum catharticum*, a locally introduced annual, becomes most abundant in July and August on one of the pastures not shown in the data. *Danthonia spicata* and *Poa compressa* sometimes show increases in mid-summer, but these generally do well to hold their own with other species in the fifth (constant) category.

4. Truly *autumnal species* are annuals. *Digitaria Ischaemum* is present on most pastures, not noticeable in the seedling stages in June but increasing greatly as the season advances, occupying in September as much as 10% of the bare space of mid-summer. *Cyperus diandrus* is similar and becomes conspicuous on some pastures in early September. *Lobelia inflata*, an annual (38), produces rosette seedlings in late summer. A few first-year plants of the biennial *Verbascum Thapsus* were found in some pastures. Seed of these four species are frequently found in a viable condition in the soil.

Many of the perennials make a second spurt of growth after August and soon occupy space greater than in June. *Trifolium repens* is noted for its fall growth. *Poa pratensis* is a grass of this type, flourishing vegetatively in September. *Phleum pratense* sometimes attempts a second flowering. *Agrostis stolonifera*, especially the variety *compacta*, proliferates again in the fall.

5. Species which tend to remain *constant* throughout the season are strong-growing, deep-rooted and drought-resistant perennials often classed as "weeds" but unjustly so for some (23). These do not produce long stolons and spread very slowly by vegetative means. Such species are *Taraxacum officinale*, *Prunella vulgaris*, *Chrysanthemum Leucanthemum*, *Ranunculus acris*, *Plantago major*, *Panicum lanuginosum*, *Carex* spp.

CONCLUSIONS

An ecological study of the flora of permanent pastures in the Cowansville district of Quebec seems to justify the following conclusions.

1. The stabilized vegetation is an association of plants of a growth-form selected by the principal biotic factor, which is the grazing animal. They are introduced perennial grasses and forbs of low or creeping habit, possessing intercalary meristem or growth points close to the ground and spreading by stolons or rhizomes.

2. The application of artificial fertilizers acts as a disturbing agent, initiating a succession in the vegetation. In the first year subsequent to treatment, legumes (chiefly *Trifolium repens*) are high, and the other

forbs and bare ground are low. In the second and third years the strong-growing grasses increase, while legumes decrease. In the fourth year the vegetation shows indications of regaining its natural composition.

3. Variations in botanical composition within the growing season are controlled by meteorological conditions (high temperature and low precipitation) in the latter part of July and August. Plants with inherent characteristics for seasonal growth have been naturally selected to these conditions in long established swards.

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Résumé

Etude des pâturages X. Suite et variation dans la composition botanique des pâturages permanents—W. G. Dore, Collège Macdonald, Qué.

Une étude écologique de la flore des pâturages permanents du district de Cowansville, Québec, paraît donner lieu aux conclusions que voici:—La végétation stabilisée se compose d'une association de plantes de la forme choisie par le principal facteur biotique, c'est-à-dire l'animal paissant. Ce sont des graminées vivaces introduites et des formes à pousse naine ou rampante, possédant un méristème intercalaire ou des points de végétation près de terre et se propageant par stolons ou rhizomes.

L'application d'engrais artificiels dérange cet ordre en provoquant une succession de végétation. Dans la première année qui suit l'application, la proportion de légumineuses (principalement le *Trifolium repens*) est forte tandis que celle des autres formes est faible. Dans la deuxième année et la troisième année, les graminées à pousse forte augmentent tandis que les légumineuses diminuent. Dans la quatrième année, la végétation commence à reprendre sa composition naturelle. Les variations de composition botanique dans les limites d'une saison de végétation sont contrôlées par les conditions météorologiques (haute température et faible condensation) vers la fin de juillet et d'août. Les plantes à caractéristiques inhérentes pour la végétation saisonnière ont été sélectionnées naturellement pour ces conditions dans les prés depuis longtemps établis.

THE INHERITANCE OF EGG PRODUCTION IN THE DOMESTIC FOWL

I. GENERAL CONSIDERATIONS¹

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The literature on the inheritance of yearly egg production and its component parts, including papers dealing with closely related topics, is rapidly becoming enormous. All or most workers agree that the progeny test is the most efficient method of selection. Beyond this, notwithstanding the numerous publications very little progress appears to have been made in the direction of a common understanding of the problem. This is well illustrated by the opposing viewpoints held by Hall (4) and Petrov (10). The former, from the results of breeding high and low line Leghorns at Cornell claims that selection on the basis of pedigree (not the progeny test) will produce marked and steady progress. Petrov, on the other hand, after a detailed examination of the same Cornell data claims that improvements in environmental conditions are mainly responsible for increased production at Cornell and that, for at least eleven years, the Cornell workers have been unable to change the genetic make-up of their flock by selection on the pedigree basis. Other conflicting views and statements prevail throughout the literature.

In this series of papers an attempt will be made to review certain fundamentals in the light of their application to the problem in hand. These general considerations will be followed by the presentation of actual data in later papers, the purpose being, in general, to build up a conception of the forces which govern variability in egg production, and in particular, to evaluate the relative part played by genetic and non-genetic forces in determining the variability. Such an evaluation is, of course, fundamental to a proper conception of the practical problem of breeding for egg production. Finally the practical significance of the conclusions arrived at will be discussed and a breeding program designed to take advantage of the facts disclosed will be enunciated. References to the practical literature in the field are not quoted in detail; *Poultry Husbandry* by Jull (7) and *Poultry Breeding* by the same author (8) are rather complete encyclopædias to literature of that type.

The literature discloses the fact that the animal geneticist has expended an enormous amount of energy in endeavours to establish techniques to be of immediate value to the practical breeder. He has expended this energy, for the most part, in earnest attempts to "discover" the exact mode of inheritance and to evaluate the nature and extent of the relationships existing between yearly egg numbers and various arbitrarily chosen components of the same. In some cases he has even proceeded to apply the final touches to his architectural design of the involved mechanism, only to find that it fails to function smoothly in the light of additional evidence.

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THEORETICAL CONSIDERATIONS

When hypothetical set-ups, involving established principles of Mendelian inheritance, are used as bases for the calculation of expected statistics and such statistics are compared with those observed in actual practice, certain information emerges which, while of no particular scientific value, does have a very considerable bearing on the practical problem of breeding for egg production. This information indicates rather definitely that experimental studies designed to establish the mode of inheritance of egg numbers are, at the present time, rather premature.

While it is true that sporadic attempts have been made to assign a finite architecture to the genes determining egg laying ability, it is the general view that the situation is somewhat more complicated than that which has been indicated. It seems probable that many hundred gene pairs directly and indirectly at one time or another play a greater or smaller part in determining the first year egg production of an individual. It is not proposed to enter into a discussion of the merits of a view which attributes the variation in egg production between individuals of a population to a small number of genetic differences and large environmental discrepancies as against one which conceives a very large number of gene differences affected very little by environment. It might be well, however, to suggest that neither of these views exhausts the possibilities. In fact it appears that the complexity of the situation, occasioned by the probable existence of a complicated interrelationship between heredity and environment, is much greater than has been recognized hitherto. This, as well as other interrelations will be discussed in the following sections.

Gene—Environment Interactions

A large body of precise information dealing with the manner in which genes ultimately come to exert their influence on the expressed character exists. The situation may be summarized as follows.

(1) Phenotypes are not solely the expression of genetic potentiality but result from a gene-environment interaction.

(2) Environmental differences affecting a whole population, as a rule, modify only the absolute expression of given characters, *i.e.*, overlapping or reversal of phenotypes is not the rule.

(3) When, however, the same genotypes occur under different environments, the situation outlined under (2) may cause phenotypic variability between the populations.

(4) Different genotypes may also be obscured under certain uniform environments.

(5) When different genotypes occur under different environments the situations outlined under (2), (3) and (4) make phenotypic expressions of certain traits almost completely unreliable as indicators of relative genetic potentialities. In fact, it is quite possible to witness a reversal of phenotypes a second season, even when the environment is common to the same genotypes within each season.

Examples pertinent to the five points enumerated above, must, of necessity, be drawn largely outside the field of egg production. The lack of precise information in this field is, in itself, an indication of the large and varied effect of environment upon the phenotype.

The first two points will be conceded. Examples of the third point can be drawn from several sources. Although the great general principles of Mendelian inheritance emerged as a result of studies on traits characterized by discontinuous variation, the discontinuous nature of the variation is not literally so. This is clear when it is pointed out that peas of Mendel's tall strain could easily be placed under environmental conditions in which they would attain a lesser height than tall peas under normal conditions. The point may be illustrated with regard to egg production by pointing out that it is quite possible by a slight alteration in feed to lower the rate of egg laying in a group of birds, below that which will be attained by a genetically similar group under optimum conditions.

A specific example of the fourth point is found in the fact that Light Sussex, which are genetically white fleshed, cannot be distinguished in so far as colour of flesh is concerned from Barred Plymouth Rocks if both breeds have been reared on rations containing neither yellow corn nor green feed. Again it is not difficult to envisage a similar situation with regard to egg production.

It appears that the fifth point can be illustrated no better than by examples drawn directly from the field of poultry breeding. Roberts and Card (12) have shown that individual birds vary in the extent of their natural resistance to "pullorum" disease and that this natural resistance depends to a considerable degree on the genotype. It would be impossible to distinguish between two strains differing widely in natural resistance to this disease if they were not exposed to infection. While specific examples are not readily forthcoming, few biologists will challenge the statement that mature fowls differ in their inherited resistance to some types of specific infection. Infectious diseases have a direct effect on the metabolic level of the individual and consequently on egg production. The relative level of egg production in two strains, therefore, will depend upon exposure or non-exposure to infection, as well as the interaction between infection and the "protective" genes. The existence of infection in a flock, therefore, will cause the masking and overlapping of the potentialities of genes which affect egg production but which are not concerned with resistance or susceptibility to disease. Likewise, the absence of infection in a flock, while producing phenotypes which are criteria of the make-up of the individuals with regard to primary egg-producing genes masks the presence or absence of genes determining resistance to infection. This obscures the relative egg-producing potentialities of the same individuals in an infectious environment.

That which holds true for certain types of infectious diseases undoubtedly holds true for adverse conditions of other kinds. For instance, it is not at all improbable that individual fowls possess an inherent tolerance to unbalanced or inadequate rations, the degree of such tolerance varying with the genotype. Thus, the growth rate of individual chicks within a group fed an inadequate ration will show considerable variation. The same group fed on an adequate ration will be more uniform. To illustrate a reversal of phenotypes only one step further need be taken. Let us suppose that the superiority of a certain family within a flock which is uniformly housed and fed during their first laying year, is due to the possession of genes which overcome a partial deficiency which exists in the feed. During the second laying year, a deficiency of another type

exists to which the better birds of the previous year are susceptible and against which the poorer birds possess "protective" genes. *The better birds of the first year may thus become the poorer birds of the second year due solely to the interaction between the genotype and the changing environment.*

These types of gene-environment interactions enormously complicate selective breeding. The practical bearing of these complications has not had sufficient recognition. The newer biometrical techniques will afford an answer to problems of this sort and undoubtedly more specific information will soon be forthcoming.

Many of the environmental conditions referred to above are subject to a considerable amount of control in so far as a flock is concerned. However, causes of individual bird variation, which are not readily controlled, exist within a flock. Some of these are: competition for feed, chance exposure to disease-infected areas and to gradients of temperature and humidity which occur within the pen, and peculiarities of the individual with regard to the relative proportions of mash and grain consumed. Environmental variation of this type exists as is evident by the fact that, under Ottawa conditions, birds allowed free choice of laying mash and scratch grain and confined in pens with littered floors show a variation of 25% in their first year egg records, while similar birds fed all mash and confined in individual cages with wire floors show a variability of only 15%. The decrease in variability is due to the fact that variation in protein intake and individual competition have been eliminated. However it must be recognized that much of the variation in the last group is still environmental. Chance variations such as these, which occur within a flock, also mask the true phenotypes and add to the difficulties of the poultry breeder.

Gene-gene Interactions

As has been implied earlier, there undoubtedly exists a large number of genes which primarily affect production. These are in addition to the genes which come into play under certain special environments. In this section we shall deal with the probable ways in which these "primary egg genes" produce their effects. The great bulk of genetic literature dealing with the inheritance of quantitative traits until recently, at least, implied that a phenotype is produced by a simple summation of the effects of individual genes. Moreover, it was generally assumed that the genes lack dominance and are independent of other genes in the effect they produce. Shull (13) pointed out that such a postulation is wholly unnecessary to explain cases of so called "blended inheritance" on a multiple gene basis. The principal argument against such a postulation appears to be the fundamental principle of gene individuality and independence itself. It would indeed be a coincidence if all the genes involved in cases of blended inheritance lacked dominance and were equal and additive in effect. As pointed out by Turner (14): "Blending inheritance may, therefore, be assumed to be caused by genes of unequal influence, some of which may be dominant, others recessive, and some lacking dominance. The usual appearance of blending in the character would then be due to the fact that only rarely are all the genes present in the parental stock in a homozygous or pure form (either dominant or recessive)."

In addition to the nature of the individual genes themselves, a critical survey of the situation affords strong evidence that the character is not produced by a simple summation of the effects of the individual genes. Rasmussen (11) has presented sufficient arguments to establish as likely the existence of gene interaction. His "interaction hypothesis" conceives that the effect of each positive gene in the genotype is dependent upon the number of other positive genes present, the visible effect of a particular one being smaller the greater the number of others acting in the same direction. Rasmussen has presented a rather commendable argument for this view and the interested reader is referred to his paper.

It appears likely that the primary egg genes do not all lack dominance nor do they produce the visible character by a simple summation of the independent effects of each. *A more modern theory is one which visualizes a heterogeneous mixture of dominants, partial dominants and recessives, producing their ultimate effect according to the law of diminishing returns, the effect on the phenotype of a specific gene depending upon the total gene "dose" carried by the genotype.*

THE PRACTICAL APPLICATION OF FUNDAMENTALS

If the above picture concerning the interaction between heredity and environment as well as between the primary egg genes is an approximation of the true situation, it is almost hopeless to attempt any sort of a specific genetic analysis of the problem. With the above situation fully in mind however, there are certain broad lines of reasoning which may be followed to a logical conclusion. In the discussions which follow the reader is asked to divorce himself from the idea that a specific analysis of the problem is being attempted and to bear in mind that evidence is being presented which has only a general bearing on the relative influence of genetic and non-genetic variation and consequently on the practical problem of breeding for egg production.

Variability and Its Relation to Mendelism

Let it be assumed that every bird, no matter how poorly equipped with egg producing genes, has the ability to lay 35 eggs per year, and that this may vary for different genotypes to a maximum of 355 eggs per year. This is practically the observed range although a very occasional record both above and below these figures will be found. Likewise let two divergent hypotheses be made; first, that the genes all lack dominance and are equal and additive in effect; second, that all genes affecting production favourably are complete dominants and are equal and additive in effect. For the time being, in both cases, it is assumed that allelomorphs occur with equal frequencies.

Curves may now be constructed under each hypothesis, upon this range as a base, illustrating the nature of and changes in the frequency distribution of a random-bred population with increasing numbers of genes. Figure 1 shows such curves under the first hypothesis and Figure 2 under the second.

When the range throughout which a character manifests itself is held constant and the number of genes affecting the character is increased, under these hypotheses, the effect of a single gene decreases. This causes

the curves to narrow and the variability therefore decreases. This decrease in variability with increasing numbers of genes is graphically illustrated in Figures 1 and 2. The standard deviation of populations under the

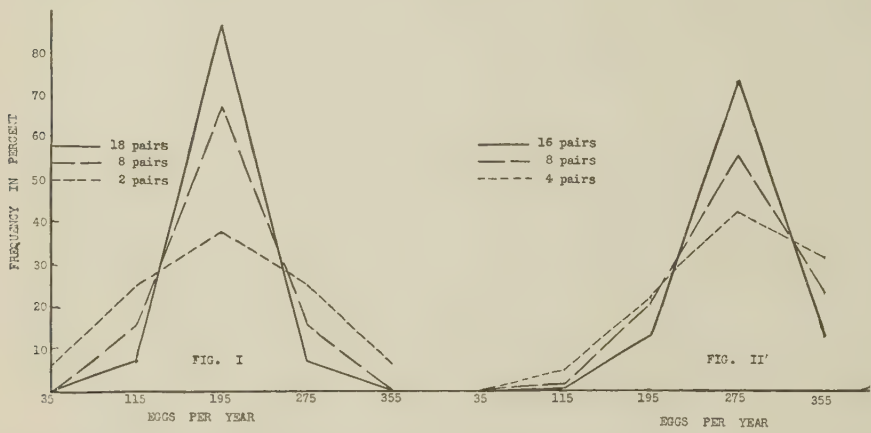


FIGURE 1.—Showing the decrease in variability of a random bred population, with respect to yearly egg numbers, as the number of genes affecting the character increases. Here the genes lack dominance and are equal and additive in effect.

FIGURE 2.—Same as figure one except that the genes are dominant but equal and additive in effect.

first hypothesis is $\sqrt{.5 \times .5 \times n}$, where n = the number of genes or twice the number of gene pairs. Likewise the standard deviation formula for populations under the second hypothesis is $\sqrt{.75 \times .25 \times n}$, where n = the number of gene pairs or half the number of genes. These formulae give the standard deviations in terms of unit classes. In order to convert it to eggs to fit our observed range of 35–355 eggs it is only necessary to multiply by the appropriate class interval expressed in eggs. Tables 1 and 2 show the decrease in variability under hypothesis 1 and 2 respectively.

It is seen that the σ 's of the populations in Table 1 are approximately 82% of those in Table 2 and that in both cases the variability decreases rapidly until with 200 or more gene pairs involved the absolute difference

TABLE 1.—SHOWING THE DECREASE IN VARIABILITY OF RANDOM BRED POPULATIONS AS THE NUMBER OF GENES INCREASE, WHEN THE GENES LACK DOMINANCE AND ARE EQUAL AND ADDITIVE IN EFFECT

Number of gene pairs	σ in unit classes	Class interval in eggs	σ in eggs	C. V.	σ as % of spread
1	0.707	160.00	113.12	58.0	35.4
2	1.000	80.00	80.00	41.0	25.0
4	1.414	40.00	56.56	29.0	17.7
8	2.000	20.00	40.00	20.5	12.5
18	3.000	8.89	26.67	13.7	8.3
50	5.000	3.20	16.00	8.2	5.0
100	7.071	1.60	11.31	5.8	3.5
200	10.000	.80	8.00	4.1	2.5
300	12.247	.53	6.49	3.3	2.0

TABLE 2.—SHOWING THE DECREASE IN VARIABILITY OF RANDOM BRED POPULATIONS AS THE NUMBER OF GENES INCREASE, WHEN THE GENES ARE DOMINANT BUT EQUAL AND ADDITIVE IN EFFECT

Number of gene pairs	σ in unit classes	Class interval in eggs	σ in eggs	C. V.	σ as % of spread
1	0.433	320.00	138.56	50.4	43.3
2	0.612	160.00	97.98	35.6	30.6
4	0.866	80.00	69.28	25.2	21.7
8	1.225	40.00	49.00	17.8	15.3
18	1.837	17.78	32.66	11.9	10.2
50	3.062	6.40	19.60	7.1	6.1
100	4.330	3.20	13.86	5.0	4.3
200	6.124	1.60	9.80	3.6	3.1
300	7.400	1.07	7.92	2.9	2.5

in the σ between tables for any given number of genes is less than 2 eggs. The rate of decrease in variance bears a constant relation to the increase in genes so that, providing the spread between the highest and lowest individual in a random bred population is known together with a measure of variability, the number of genes involved can be calculated for each hypothesis. When dominance is lacking the number of genes is

$$\frac{\Delta^2}{8V}$$

where Δ = spread between highest and lowest individual and V = variance = σ^2 .

When dominance prevails the number is

$$\frac{\Delta^2}{5.333V}$$

These formulae will yield the number of genes involved providing that all variation is genetic. In traits where genetic and non-genetic variation occurs the number of genes under hypothesis 1 can be arrived at by

$$\frac{\Delta^2}{8(V_{F2} - V_{F1})}$$

where V_{F2} and V_{F1} = variance of the F_2 and F_1 respectively, and Δ = the difference between the two parental strains. These parental strains must be homozygous and lie at the two extremes. This method of calculating the number of genes involved in quantitative traits was mentioned by Castle (1) who proposed a formula, but later the same author (2) on the suggestion of Wright, modified it to read as above.

With regard to egg production it is not possible to secure homozygous high and low parents, and therefore not possible to secure a measure of non-genetic separate from genetic variability. The σ which characterizes populations under Canadian conditions is approximately 42 eggs. This is the average variability exhibited by Canadian contest populations. If all variation in egg numbers is treated, for the time being as genetic, and the formulae given above are applied, we find under hypothesis 1 that

approximately 6 gene-pairs are involved, while under hypothesis 2 there are about 9 pairs. Apart from the fact that all variation is not genetic there are a number of other objections to the use of such a method of gene estimation; in the first place it is obvious that the actual nature of the genes will not comply with the conditions of either hypothesis; secondly it may be argued that the contest populations are not strictly random bred; thirdly, if Rasmussen's hypothesis of gene interaction is correct the formulae are not applicable; fourthly, the existence of secondary genes which interact with specific environments will invalidate the method.

Using the same formula and logic but approaching the problem from a different angle, our purpose can be served equally well without leaving the method open to the same degree of criticism. As previously intimated there undoubtedly exist at least 200 or 300 gene-pairs. Supposing that none but genetic variation existed and substituting in the proper equation we have for 200 pairs under hypothesis 1

$$V = \frac{\Delta^2}{8n}$$

$$V = \frac{(320)^2}{8 \times 200}$$

$$V = 64 \text{ or } \sigma = 8.$$

For 300 pairs under hypothesis 1

$$V = \frac{(320)^2}{8 \times 300}$$

$$V = 42.66 \text{ or } \sigma = 6.5.$$

For 200 pairs under hypothesis 2

$$V = \frac{(320)^2}{5.333 \times 200}$$

$$V = 96 \text{ or } \sigma = 9.8.$$

For 300 pairs under hypothesis 2

$$V = \frac{(320)^2}{5.333 \times 300}$$

$$V = 64 \text{ or } \sigma = 8.$$

From this it appears that genetic variance can hardly exceed 130 and is more likely to be 50 or even less.

The objections listed above to the former method of gene estimation do not apply to the same degree or as rigorously to this latter method of estimating genetic variance. Since the statistics of observed populations, other than the range within which yearly egg production falls, is not being used, degrees of departure from the random bred state, or other idiosyncrasies which may characterize certain populations are not objections. Again, while it is true that the genes will not conform strictly to either hypothesis, a mixture of dominants, recessives and partial dominants will not produce a variance greatly different from either hypothetical set-up.

As a matter of fact, for any given number of genes, the actual genetic variance should fall somewhere between that calculated for the two.

If gene interaction exists, or if the allelomorphs do not occur with equal frequencies, the variance will be smaller than that indicated by the formulae. In fact if one allelomorph in each of several gene pairs is extremely rare—as (.99 *B* + .01 *b*)—the variance produced by a given number of genes will be enormously decreased. On the other hand, the existence of secondary genes which come into play under special environments, assuming that their numbers are small for each type of environment, would tend to increase the variance. In fact if 3 or 4 secondary genes have very large effects, the variance would be enormously increased. Secondary genes, then, tend to offset unequal allelomorph frequencies in the foregoing estimates. Undoubtedly these various factors vary considerably from flock to flock and singly or in combination have marked effects on the genetic variance; in some flocks the variance would be greater, in other flocks less than that indicated by the formulae. *All things considered it would appear that genetic variance can hardly exceed 500 and in some flocks may be considerably less. In any case it must be a relatively small fraction of the total observed variance.*

If we allow a genetic variance of 500, then variance due to the environment must be the difference between this and the total variance actually observed, or $1764 - 500 = 1264$. *In other words, gene segregation and recombination is responsible at the most for only 25 to 30% and in some cases probably as low as 10% of the variance which characterizes a laying flock.*

Stability of Mendelian Populations

Pearson (9) first pointed out that an F_2 Mendelian population conforming to a 1 : 2 : 1 ratio maintained equilibrium in subsequent generations when mating occurred at random. Hardy (5) first drew attention to the fact that regardless of the phenotypic ratio or the proportions of the various genes, equilibrium is reached when mating occurs at random, and subsequently in the absence of selection the state of equilibrium is maintained from one generation to another. Further it may be stated, in so far as a single gene pair is concerned: First, the state of equilibrium is reached when the square of half the frequency of the heterozygous class equals the product of the frequencies of the two homozygous classes; second, this state of equilibrium is attained in a single generation of random mating.

In accordance with the first statement above and letting a = frequency of the homozygous dominant and b = frequency of homozygous recessive, the proportions of the dominant, heterozygous and recessive classes respectively, in the equilibrium state are

$$a^2 : 2ab : b^2$$

To express the frequencies as fractions of unity so that $a^2 + 2ab + b^2 = 1$, we may write the equilibrium state as

$$a^2 : 2a(1 - a) : (1 - a)^2$$

Any F_2 generation resulting from an original cross of two pure lines will conform to the above formula, and likewise it can be shown that any

F_2 generation involving a larger number of genes is in equilibrium and in the absence of selection will maintain that state. If efficient selection is subsequently practised upon such a random bred population, the frequency curve representing the distribution of the random population will in subsequent generations exhibit skewness; this skewness will be in the direction in which selection has been practised and the degree of skewness will increase in each succeeding generation. At the same time the variation of the successive generations will consistently decrease.

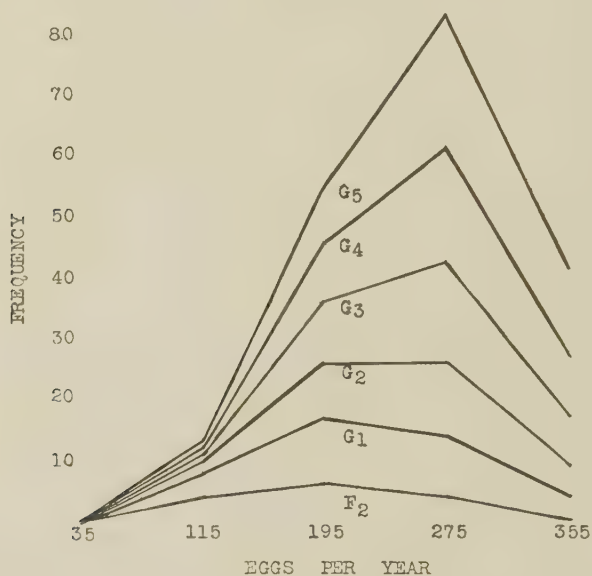


FIGURE 3.—Skewness characterizing the distribution of successive generations when phenotypic selection is practised on the female side only. The curves are drawn for two pairs of genes lacking dominance.

Figure 3 shows the skewness which successive generations will exhibit if egg production depends on two pairs of genes lacking dominance and only females laying 195 eggs or over are used as breeders, the males being picked at random. The males would of course, after the first parental generation, actually be the sons of females laying 195 eggs or more.

TABLE 3.—SHOWING MEANS, STANDARD DEVIATIONS AND COEFFICIENTS OF VARIABILITY OF SUCCESSIVE GENERATIONS WHEN MONOSEXUAL PHENOTYPIC SELECTION IS PRACTISED AND WHEN ONE AND TWO GENE PAIRS ARE INVOLVED

Generation of Selection	One pair			Two pairs		
	Mean	σ	C.V.	Mean	σ	C.V.
F 2	195.0	113.0	58.0	195.0	80.0	41.0
G 1	221.6	109.9	49.6	216.8	75.0	34.6
G 2	240.3	107.6	44.8	231.1	73.4	31.7
G 3	255.0	104.4	40.9	241.7	72.2	29.9
G 4	266.6	99.2	37.2	250.2	71.1	28.4
G 5	276.0	97.3	35.3	257.1	70.3	27.3

Table 3 shows the means, standard deviations and coefficients of variability of successive generations when this type of selection is practised for hypothetical set-ups of both 1 and 2 gene-pairs. It is seen that less rapid progress is made in increasing the mean production under the 2-gene-pair hypothesis. The greater the number of gene-pairs involved the less rapidly will desired results accrue from selection. This is illustrated graphically in Figure 4.

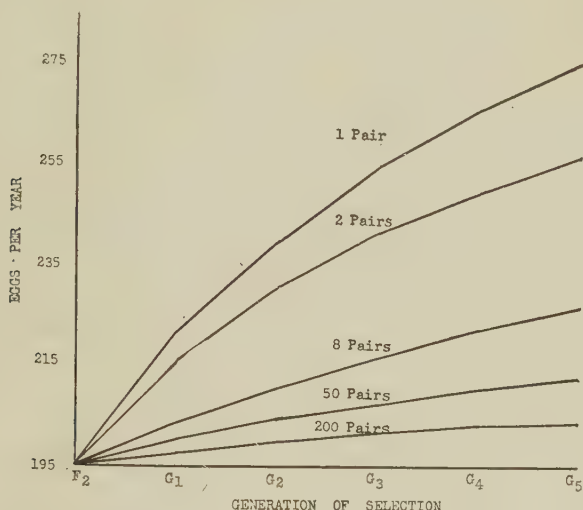


FIGURE 4.—Increase shown by successive generations of phenotypic selection on the female side only, when different numbers of gene pairs are involved.

It is seen that the rate of increase is greatest in the first generation of selection and constantly diminishes in succeeding generations. In the figure, curves are shown for 1, 2, 8, 50, and 200 gene-pairs. In the case of 1 and 2 pairs actual computations have been made for 5 generations, whereas in the other cases the curves are based on actual computation for 1 generation only, after which, due to the laborious calculations involved the curves have been extended to 5 generations by inspection.

Where large numbers of genes are involved, the increase which one can expect to secure by monosexual phenotypic selection is extremely small particularly after the first 2 or 3 generations. This is true when all variation is genetic. Where genetic variation is obscured by that due to the environment, as is actually the case in egg production, progress would be considerably slower. Since monosexual phenotypic selection is that chiefly relied upon by poultry breeders, and as considerable environmental variation undoubtedly exists in egg production, one can expect very little if any progress in improving the genotype by this method.

The Method of Variance Applied to Mendelian Populations

The newer statistical technique of variance is becoming increasingly popular with animal biologists and promises to be of considerable assistance to the geneticist. In connection with egg production it can be used to particular advantage since it affords a more specific measure of the relative

influence of heredity and environment than can be arrived at by other methods.

Where parents are unrelated or where mating occurs at random the correlation between the gene make-up of offspring and father as well as between offspring and mother is .5. Each parent therefore determines $\frac{1}{4}$ of the variance of the offspring. Consequently a total of $\frac{1}{2}$ of the variance is determined between families leaving $\frac{1}{2}$ of the variance within families. When the genes lack dominance, and are equal and additive in effect, the above relationships in gene make-up are extended to the phenotype. The analysis of variance into genetic and non-genetic components and the relation of the genetic component to intra-familial variance was first elucidated by Weinberg (15) and later confirmed and extended by Fisher (3), who went into considerable detail concerning the effect of different genetic postulations on the variance ratio. For the information of practical geneticists who may have difficulty in following Fisher's analysis this may be shown as follows when $a^2 : 2a(1 - a) : (1 - a)^2$ is the ratio of the frequencies of the three genotypes and when the difference in value of the two homozygous classes is reduced to unity and the value of the heterozygote is expressed as a fraction of unity and where $d = \frac{1}{2}$ = the difference between phenotypic value of Bb and bb :

Males $\times$ Females		Offspring, frequency type	Family variance
$a^2 \ BB$	$a^2 \ BB$	$a^4 \ BB$	0
	$2a(1 - a) \ Bb$	$a^2[2a(1 - a)] \ BB + Bb$	$\frac{d^2}{4}$
	$(1 - a)^2 \ bb$	$a^2(1 - a)^2 \ Bb$	0
$2a(1 - a) \ Bb$	$a^2 \ BB$	$a^2[2a(1 - a)] \ BB + Bb$	$\frac{d^2}{4}$
	$2a(1 - a) \ Bb$	$4a^2(1 - a)^2 \ BB + 2Bb + bb$	$\frac{d^2}{2}$
	$(1 - a)^2 \ bb$	$2a(1 - a)^3 \ Bb + bb$	$\frac{d^2}{4}$
$(1 - a)^2 \ bb$	$a^2 \ BB$	$a^2(1 - a)^2 \ Bb$	0
	$2a(1 - a) \ Bb$	$2a(1 - a)^3 \ Bb + bb$	$\frac{d^2}{4}$
	$(1 - a)^2 \ bb$	$(1 - a)^4 \ bb$	0

Average variance within families equals

$$\frac{\frac{d^2}{4}(2a^3 - 2a^4) + \frac{d^2}{4}2a(1 + a - 4a^2 + 2a^3) + \frac{d^2}{4}(2a - 6a^2 + 6a^3 - 2a^4)}{a^2 + 2a(1 - a) + (1 - a)^2}$$

This will further reduce to

$$d^2a(1 - a)$$

Substituting for the value of d

$$\frac{1}{4}a(1 - a).$$

The mean value of the random bred population is

$$\frac{d[2a(1-a)] + a^2}{a^2 + 2a(1-a) + (1-a)^2} = d[2a(1-a)] + a^2$$

The sum of the squared values is

$$d^2[2a(1-a)] + a^2$$

Substituting in the usual formula for the variance we have for the total variance of the random bred population

$$d^2[2a(1-a)] + a^2 - [d\{2a(1-a)\} + a^2]^2$$

Substituting for the value of d and reducing we have

$$\frac{1}{2}a(1-a)$$

The ratio of variance within families to total variance therefore is $\frac{1}{4}a(1-a) : \frac{1}{2}a(1-a)$ or $1 : 2$. *When the genes lack dominance, therefore, and are equal and additive in effect, the variance within full sibs will be just half the total variance.*

When $d = 1$, or in other words when complete dominance prevails, the correlations between the actual gene make-up of parent and offspring do not extend to the expressed character. This lowers the correlations and causes more than half of the variation to occur within sibships.

When analysed in the manner of the preceding case the formula for variance within families equals

$$a(1-a)^2 \frac{(4-a)}{4}$$

while that for the variance of the total population is

$$a(1-a)^2 (2-a)$$

The ratio of within family: total variance in this case varies with varying values of a . When $a = \frac{1}{2}$ the ratio has a value of $1 : 1.714$. This ratio narrows as a increases and widens as a diminishes until with values for a of 1 and 0.1 the ratios are $1 : 1$ and $1 : 1.948$ respectively.

In the case of complete dominance then, unless a varies considerably from a value of $\frac{1}{2}$, the variance within full sibs should be slightly more than half the total variance. When a varies from $\frac{1}{2}$ the frequency curve for the population will be skewed and in cases where one gene pair is involved the value of a may be definitely calculated.

These ratios hold good for any number of genes, providing the effects of the genes are independent. The effect of gene interaction, of the type described by Rasmusson (11), is to decrease the absolute value of both within family and total variance, while the ratio of the two becomes narrower than $1 : 2$. The exact degree to which the within-family variance exceeds half the total variance depends upon the degree of gene interaction, but in any case, providing the distribution is not decidedly skewed, it should be slight and the ratio generally comparable to the case of dominance.

Here then is a fundamental fact which can be capitalized on in connection with the practice of breeding for egg production. If one analyses, biometrically, the variation of populations which have been allowed to

breed at random for at least one preceding generation and separates from the total variance that which occurs on the average within full sisters, a fairly close, although not exact, measure of the relative proportions of genetic and non-genetic variability can be arrived at.

According to the foregoing analysis, in cases where all variation is genetic the variance secured within full sisters should be at least half the total variance. If g^2 = total genetic variance and e^2 = variance due to all other causes (environment), then the total variance is $g^2 + e^2$ while the variance within families, which in the case of egg production would be full sisters, is $\frac{g^2}{2} + e^2$.

Since the difference between the two is $\frac{g^2}{2}$, it follows that g^2 or *the total genetic variance is twice the difference between the total and within-family variance.*

With such a relationship established it seems a simple matter by the proper collection and analysis of data to set up a balance sheet of genetic and environmental influences. Considerable care, however, must be exercised in the use of the method. Hogben (6) in a commendable monograph has drawn attention to the pitfalls which beset the application of statistical technique in the study of human inheritance and has pointed out that faultless logic and mathematics may not be applicable in practice because the assumptions upon which they rest do not correspond to actuality. Several pertinent examples are cited by Hogben to show that a uniform environment does not necessarily reduce total variability and may not increase the proportional effect of genetic factors on the total variability. This is on account of the interaction of the genotype with the environment which has been pointed out as applying to the expression of egg laying ability.

The ratio of variance within families to total variance can be used as a technique for the calibration of genetic and environmental variation only when the environmental discrepancies are as likely to occur between members of the same family as between members of different families.

In viviparous animals which live in family groups for at least a portion of their life history, the environmental variations which occur between families is far greater both before and after birth than those which occur within the family. This will invalidate correlation and variance technique in so far as they may be used to evaluate heredity and environment. In domestic fowl we are dealing with an oviparous animal, which, when reared artificially in large groups under modern methods of incubation and brooding and confined in large laying pens with no conscious grouping of family units, comes close to fulfilling a condition of randomized environment.

The greatest objection to the use of the variance method in estimating the proportion of genetic variance is the fact that the relatively small number of males used at any one poultry farm is hardly sufficient to insure their randomization. This necessitates the inclusion of several farms in order to insure a fair sample of male genotypes. Since, on the average, greater environmental differences exist between two members of different farms than between two members of the same farm it has the effect of stratifying

the total population into groups between which there may be wide environmental differences. Since the use of individual males is confined to one group, the correlation between genotypes within the groups will be greater than the same correlation between the groups. This will have the effect of increasing the total variance and therefore of lowering the proportion of the total variance which occurs within families. Fortunately the method of variance allows us to subtract from the total variance that which is due to differences between farms and allows us to estimate the average variance of several farms without including therein differences due to location. The objection which remains is one which concerns the interaction between genotype and environment. On this account the total variability and the fractions thereof which are secured by grouping a large number of farms may not be of the same order as would be the case if all birds were housed in the one locality and exposed to the same general environment. However, data collected in this way will provide an estimate of total variance which should be typical of the interaction of the genotype to the average environment. Likewise the within-family variance should be a representative measure of the average spread within a family under average environmental conditions.

In a detailed analysis of breeding records from seven Canadian Experimental Farms the results of which will be subsequently published the average total variance was found to be 1,713 eggs while the average variance within families of full sisters was 1,496. According to previous arguments the total genetic variance is $2(1,713 - 1,496) = 434$. This is 25.3% of the total. The corresponding σ is

$$\sqrt{434} = 20.83$$

Here then is experimental evidence which, while open to objections, does indicate approximately the relative effect of heredity and environment and in this respect confirms the previous estimate based on theoretical grounds.

A further objection to the use of figures collected from Experimental Farm flocks for this type of analysis is the fact that the flocks are perhaps not strictly random bred. In most cases females laying at least 200 eggs per year have been used as breeders, while the males used are sons of such hens. It has been pointed out previously that this method of selection will have, theoretically, very little effect in increasing egg production and we would, therefore, not expect the farm flocks to be far from the random bred state of equilibrium.

DISCUSSION

A general consideration of the possible and probable nature of the mechanism which governs variability in egg production indicates rather definitely that it is much more complex than is generally considered. This complexity is due primarily to the fact that non-genetic or environmental influences cause a greater proportion of the variation between individuals and between families than does inheritance; the mechanism may be confounded further by an interaction between the genotype and environment which causes a reversal of phenotypes under a very slight change in environment.

This general view of the situation immediately suggests that selective breeding for the purpose of improving the productive capacity of the hen must be an extremely difficult matter. In fact it would appear that the methods of selection which have been almost entirely relied on by the great majority of breeders viz., selection of the individual on performance and pedigree must be generally unproductive of results. Nevertheless the egg producing ability of the hen has been enormously increased during the last twenty years. This fact must be reconciled in some way with the theoretical deductions drawn in this paper. Either the increase is due to non-genetic causes or our theoretical deductions have been incorrect. There is the further possibility that the inheritance of egg producing ability is not Mendelian in nature. It seems hardly necessary to entertain the third possibility without first exhausting the others. The following paper in this series will examine in some detail the increase which has occurred in production and discuss its probable causes.

ACKNOWLEDGMENTS

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SUMMARY

1. The possible and probable ways in which genes may effect egg production has been reviewed. A composite picture of the involved mechanism is visualized and appears so complex as to prohibit in the present state of knowledge a specific analysis of the mode of inheritance either of yearly egg production or of its component parts.

2. Evidence is presented which indicates a gene-gene as well as a gene-environment interaction.

3. The stability of Mendelian populations in the absence of selection is pointed out and the direction and rate of change which is produced in such populations by certain popular methods of selection and with varying numbers of involved genes is discussed.

4. The amount of variability exhibited by Mendelian populations characterized by different hypothetical set-ups is shown and statistical methods of estimating the approximate influence of genetic and non-genetic influences pointed out. The application of these methods to actual data indicate that only 20-25% of the observed variance of populations is due to gene segregation and recombination.

5. The practical implications of the above points are dealt with and it is concluded that selection by the phenotype and pedigree as practised by the majority of breeders can hardly produce results sufficiently positive to justify the expense involved in trapnesting and individual pedigreeing.

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Résumé

La transmission héréditaire de l'aptitude à la ponte chez les volailles domestiques, S. S. Munro, Ferme expérimentale fédérale, Ottawa, Ont.

L'auteur de cette étude passe en revue les façons possibles et probables dont les gènes peuvent affecter la ponte; il expose le mécanisme par lequel cette influence se fait sentir et déclare que ce mécanisme paraît si compliqué qu'il serait impossible, dans l'état actuel de nos connaissances, de faire une analyse spécifique du mode de transmission héréditaire de la production annuelle des œufs ou de ses parties constituantes. Les preuves recueillies indiquent qu'il y a une action réciproque entre les gènes ainsi qu'entre les gènes et le milieu. L'auteur souligne la stabilité des populations Mendéliennes, en l'absence de la sélection, et la direction et la rapidité du changement que produisent dans ces populations certaines méthodes populaires de sélection et la présence d'un nombre variable de gènes. Il expose la variabilité exhibée par les populations Mendéliennes, caractérisée par différents cadres hypothétiques, et donne des méthodes statistiques pour l'évaluation de l'influence approximative exercée par les agents génétiques et non-génétiques. L'application de ces méthodes aux données actuelles indique seulement de 20 à 25 pour cent de la variation observée dans les populations est due à la ségrégation et à la recombinaison des gènes. Il passe en revue les implications pratiques découlant des points qui précèdent et conclut que la sélection basée sur le phénotype et le pedigree, que pratique la majorité des éleveurs, ne peut guère produire des résultats suffisamment positifs pour justifier les frais qu'entraîne le contrôle au nid-trappe et l'inscription du pedigree individuel.

CEREAL RUST LOSSES IN WESTERN CANADA¹

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INTRODUCTION

Stem rust (*Puccinia graminis* Pers.) has been an important cause of economic loss during the present century in Western Canada. During the 11-year period 1925-1935, a graded series of stem-rust infections was obtained each year in field plots at Winnipeg, and annual losses in grain yield and quality of wheat and oats due to stem rust were determined. The data from these experiments have been used to increase precision in the estimation of field losses from stem rust in Manitoba and Saskatchewan. A summary of these estimations are presented in this paper.

METHOD OF ESTIMATION

The method by which these estimations were arrived at has been set forth in a previous paper (6). Briefly stated, it consisted in varying the intensity of stem-rust infection in individual plots by the application of sulphur dust to the plots at different rates and time-intervals, and in correlating the amount of rust and yield in a single standard cereal variety. Complete details of the sulphur dusting experiments, the results of which furnish the basis of the estimations presented here, are given by Bailey and Greaney (1, 2) and Greaney (3, 4, 5). Each year the reduction in yield corresponding to a known increase in the percentage infection of stem rust was computed, and a percentage-loss value giving the reduction in yield for each 10% increase of stem rust was determined. For the estimation of the annual field losses from stem rust, the average amount of rust infection and the actual yield of the crop in a given district were obtained. In the present study the percentage-loss values obtained at Winnipeg were applied to these rust and yield data for Manitoba and Saskatchewan.

While the method has the merit of being based on the results of controlled experiments, it is subject to certain sources of error. For instance, it has been established that the development of leaf rust of wheat, crown rust of oats, and some minor leaf and stem diseases, as well as stem rust, is prevented by heavy and frequent applications of sulphur dust to growing cereal plants (4). Leaf rust of wheat was very prevalent in Manitoba and Saskatchewan in 1925, 1927, and 1933, and crown rust of oats in Manitoba in 1935. Although during this period there was no appreciable development in Manitoba and Saskatchewan of leaf and stem diseases of cereals other than rusts, it must be assumed that slight reductions in yield, and possibly in grain quality, were caused by some of the minor leaf and stem diseases of wheat and oats. Nevertheless, the results of sulphur dusting experiments demonstrate clearly that annual losses in yield and grain quality suffered at Winnipeg during these years were very largely due to the presence of stem rust.

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Estimates of annual losses in yield and in grain quality, based on acreage, yield, and price statistics for Manitoba and Saskatchewan, are discussed separately in this paper.

LOSSES IN YIELD

Stem rusts of wheat and oats were almost completely controlled each year at Winnipeg in plots of Marquis wheat and Victory oats which were dusted heavily and frequently with sulphur dust. The annual yield in bushels of the dusted (rust-free) plots of Marquis wheat, and the yield of Marquis wheat plots that remained undusted (rusty) are presented in Table 1.

Yields of heavily dusted and undusted plots of Victory oats, showing the annual losses caused by stem rust at Winnipeg during the 6-year period 1929-1934, are given in Table 2.

An examination of the yield losses in Tables 1 and 2 reveals a very great variation in the amount of rust loss from year to year. In 1925, 1927, 1930, and 1935, when stem rust of wheat occurred in epidemic form in Western Canada, very heavy losses in yield were sustained at Winnipeg. Severe loss to oats occurred in 1930, and to a lesser extent in 1931 and 1934.

TABLE 1.—ANNUAL LOSSES IN YIELD OF MARQUIS WHEAT CAUSED BY RUST AT WINNIPEG, MAN., 1925-1935 (BUSHELS PER ACRE)

Year	Rust-free	Rusted	Loss ¹
1925	55.0	12.5	42.5
1926	45.0	42.0	3.0
1927	48.8	12.2	36.6
1928	35.0	22.0	13.0
1929	29.0	24.5	4.5
1930	30.4	6.1	24.3
1931	22.8	9.4	13.4
1932	48.2	31.2	17.0
1933	15.7	15.5	0.2
1934	33.4	19.8	13.6
1935	22.0	4.7	17.3
11-year average	35.0	18.2	16.8

¹ Yield difference in 1926, 1929, and 1933 not statistically significant.

TABLE 2.—ANNUAL LOSSES IN YIELD OF VICTORY OATS CAUSED BY RUST AT WINNIPEG, MAN., 1929-1934 (BUSHELS PER ACRE)

Year	Rust-free	Rusted	Loss ¹
1929	65.1	59.0	6.1
1930	74.8	29.5	45.3
1931	45.3	23.8	21.5
1932	65.6	56.4	9.2
1933	48.6	48.3	0.3
1934	60.2	43.2	17.0
6-year average	59.9	43.4	16.6

¹ Yield difference in 1929 and 1933 not statistically significant.

From 1925-1935 the average annual rust loss in percentage of the possible yield of wheat in Manitoba and Saskatchewan was 10.8%. From 1929-1934 the oat crop suffered an annual loss of 5.5%. If these losses are evaluated in terms of bushels and dollars, the economic significance of stem rust in the Prairie Provinces can be more clearly appreciated. Annual crop loss estimates in bushels

and dollars for Manitoba and Saskatchewan, computed on the basis of the percentage-loss values sustained at Winnipeg, are given in Tables 3 and 4.

TABLE 3.—ESTIMATED ANNUAL LOSSES IN BUSHEL AND DOLLARS FROM STEM RUST OF WHEAT SUSTAINED BY GRAIN GROWERS OF MANITOBA AND SASKATCHEWAN DURING THE 11-YEAR PERIOD, 1925-1935

Year	Loss in bushels (000)			Loss in dollars ¹ (000)		
	Man.	Sask.	Man. and Sask.	Man.	Sask.	Man. and Sask.
1925	54,453	57,540	111,993	66,433	68,473	134,906
1926	1,962	1,177	3,139	2,139	1,236	3,375
1927	18,891	71,192	90,083	20,024	69,768	89,792
1928	6,531	8,538	15,069	6,008	6,403	12,411
1929	4,640	3,149	7,789	4,918	3,212	8,130
1930	36,793	18,108	54,901	18,764	7,062	25,826
1931	7,895	4,848	12,743	3,237	1,745	4,982
1932	2,220	1,231	3,451	844	394	1,238
1933	000	000	000	000	000	000
1934	1,953	2,331	4,284	1,269	1,282	2,551
1935	30,674	56,571	87,245	21,472	33,943	55,415
11-year average	15,092	20,426	35,518	13,192	17,592	30,784

¹ Based on prices received by producers. Statistical Data Supplementary to the Agricultural Situation and Outlook, 1936. The Dominion Bureau of Statistics and the Dominion Department of Agriculture, Co-operating, December, 1935.

The average annual loss in wheat sustained by the grain growers of Manitoba and Saskatchewan from 1925-1935 was 35,518,000 bushels. This represented a direct loss of \$30,784,000. During the six years 1929-1934 the average annual loss from oat stem rust was 8,334,000 bushels, reducing the income of the farmers of Manitoba and Saskatchewan \$2,041,000 annually. Annual field losses have not been computed for Alberta. A conservative estimate of the annual loss sustained by grain growers in the three Prairie Provinces from rust during the past eleven years, due to reduction in yield alone of wheat and oats, is \$35,000,000.

TABLE 4.—ESTIMATED ANNUAL LOSSES IN BUSHEL AND DOLLARS FROM STEM RUST OF OATS SUSTAINED BY GRAIN GROWERS OF MANITOBA AND SASKATCHEWAN DURING THE 6-YEAR PERIOD, 1929-1934

Year	Loss in bushels (000)			Loss in dollars ¹ (000)		
	Man.	Sask.	Man. and Sask.	Man.	Sask.	Man. and Sask.
1929	3,118	4,256	7,374	1,684	2,128	3,812
1930	25,507	4,552	30,059	5,356	683	6,039
1931	6,202	2,021	8,223	1,178	364	1,542
1932	1,795	500	2,295	251	65	316
1933	000	000	000	000	000	000
1934	1,408	649	2,057	451	82	533
6-year average	6,338	1,996	8,334	1,487	554	2,041

¹ Based on prices received by producers. Statistical Data from the Dominion Bureau of Statistics and the Dominion Department of Agriculture, Co-operating, December, 1935.

LOSSES IN GRAIN QUALITY

The presence of a large proportion of small, shrunken kernels influences directly the weight per measured bushel of grain and reduces its market value. It has been found that bushel weight is significantly negatively associated with yield and constitutes a definite index of the extent of rust injury (6). The results of rust-control experiments made at Winnipeg indicate that losses in grain quality from stem rust are of great economic importance (Tables 5 and 6).

TABLE 5.—ANNUAL LOSSES IN GRAIN QUALITY OF MARQUIS WHEAT, AS INDICATED BY BUSHEL WEIGHT AND COMMERCIAL GRADE, CAUSED BY RUST AT WINNIPEG, MAN. (1925-1935)

Year	Rust-free		Rusted		Loss in bushel weight
	Bushel weight	Commercial grade	Bushel weight	Commercial grade	
	lb.	(Manitoba)	lb.	(Manitoba)	lb.
1925	63	1 Nor.	46	Feed	17
1926	60	1 Nor.	60	1 Nor.	0
1927	58	3 Nor.	45	Feed	13
1928	60	2 Nor.	59	2 Nor.	1
1929	64	1 Hard	63	1 Hard	1
1930	61	1 Hard	41	Feed	20
1931	64	1 Hard	51	No. 5	13
1932	64	1 Nor.	59	2 Nor.	5
1933	65	1 Hard	65	1 Hard	0
1934	65	2 Nor.	61	3 Nor.	4
1935	63	3 Nor.	50	6 Special	13
11-year average	62.4	—	54.5	—	7.9

Stem rust reduced the weight per measured bushel of Marquis wheat from 61 to 41 pounds in 1930. In 1927, 1931, and 1935 bushel weight was reduced 13 pounds by rust. In 1930 and 1931 the quality of the oat crop of Manitoba was appreciably lowered by stem rust.

TABLE 6.—ANNUAL LOSSES IN GRAIN QUALITY OF VICTORY OATS, AS INDICATED BY BUSHEL WEIGHT AND COMMERCIAL GRADE, CAUSED BY RUST AT WINNIPEG, MAN. (1929-1934)

Year	Rust-free		Rusted		Loss in bushel weight
	Bushel weight	Commercial grade	Bushel weight	Commercial grade	
	lb.	(Manitoba)	lb.	(Manitoba)	lb.
1929	37	2 C.W.	37	2 C.W.	0
1930	35	1 Feed	26	2 Feed	9
1931	36	2 C.W.	30	2 Feed	6
1932	42	2 C.W.	40	2 C.W.	2
1933	38	2 C.W.	38	2 C.W.	0
1934	40	2 C.W.	36	2 C.W.	4
6-year average	38.0	—	34.5	—	3.5

The difficulties in evaluating the many factors involved in the reduction of quality of small grain crops are too great to make possible close approximations of the annual loss in grain quality caused by stem rust. The commercial significance of this loss, however, is well brought out by an examination of the grain inspection records of the Western Grain Division, Winnipeg, Man. Wheat inspection records for August, September, and October of 1933, 1934, and 1935, are summarized in Table 7.

TABLE 7.—SUMMARY OF WHEAT INSPECTION RECORDS (WESTERN DIVISION).
AUGUST, SEPTEMBER AND OCTOBER, 1933, 1934 and 1935
(DOMINION BUREAU OF STATISTICS)

Red Spring Wheat Grades	1933		1934		1935	
	Number of cars	Per cent of total	Number of cars	Per cent of total	Number of cars	Per cent of total
1 Man. Hard	3,463	5.8	3,968	6.6	2,180	3.4
1 Man. Nor.	29,351	48.9	25,085	41.7	17,569	27.8
2 Man. Nor.	19,593	32.6	15,857	26.3	8,561	13.6
3 Man. Nor.	2,195	3.6	3,854	6.4	7,968	12.6
4 Man. Nor.	988	1.6	3,274	5.4	7,690	12.1
Number 5	420	0.7	2,359	3.9	4,744	7.5
Number 6	116	0.2	697	1.2	2,245	3.5
Feed	25	—	145	0.2	5,087	8.0
Other grades	3,889	6.6	5,030	8.3	3,079	4.9
No. 4 Special	—	—	—	—	1,854	2.9
No. 5 Special	—	—	—	—	1,214	1.9
No. 6 Special	—	—	—	—	1,169	1.8
Total	60,040	100.0	60,269	100.0	63,360	100.0

Of the total number of wheat cars examined in 1933, a year when rust was a negligible factor in crop production, 87.3% were graded 1 Manitoba Hard, 1 Manitoba Northern, and 2 Manitoba Northern. The 1933 wheat crop was of excellent quality. In 1934 the number of cars in the three high grades was reduced to 74.6%. The occurrence of a moderate infection of stem rust in several districts of Manitoba was, no doubt, partly responsible for the reduction in quality of the 1934 wheat crop. Of the total number of cars inspected in August, September, and October of 1935, only 44.8% graded 1 Manitoba Hard, 1 Manitoba Northern, and 2 Manitoba Northern. Furthermore, it was necessary in 1935, in order to market the large quantity of small, shrunken, low-grade rusted wheat, to institute three special grades.

The results of rust-control experiments were used as a basis for estimating crop losses from rust due to reduction in grain quality. The average annual loss in bushel weight at Winnipeg for the 11-year period 1925-1935 was approximately 8 pounds, representing a reduction of at least two commercial grades (Table 5). For the purpose of estimating the annual dollar loss in Manitoba and Saskatchewan due to reduction in commercial grade, it was assumed that 50% of the average annual wheat production of these two provinces suffered a loss of one grade from rust injury. This reduction of one grade represented a loss in price of two cents per bushel. Computed on this basis, the annual loss to the wheat growers of Manitoba and Saskatchewan was \$2,070,400. In spite of its admitted limitations,

this estimate must be considered a very conservative one, for stem rust of wheat occurred in epidemic form in four of the eleven years 1925 to 1935.

The economic losses from reduced grain quality caused by rust are much greater than this direct annual loss of approximately \$2,000,000. They include also the additional loss involved in the lowering of the general high quality of Canadian wheat on the markets of the world.

SUMMARY

From the results of controlled experiments it is estimated that, during the 11-year period 1925-1935, the grain growers of Manitoba and Saskatchewan lost annually from stem rust 10.8% of the possible wheat crop yield. This represents a direct loss of 35,518,000 bushels, the value of which reached the substantial amount of \$30,784,000. The average annual loss to the oat crop of Manitoba and Saskatchewan for the 6 years 1929-1935 was 5.5% of the possible yield, or 8,334,000 bushels. This resulted in the annual income of the grain growers being reduced \$2,041,000. Rust losses were not computed for Alberta.

Another important source of loss from rust is the reduction in grain quality. If rust losses are to be evaluated in terms of money, the market price of the grain as well as the actual loss in yield must be considered. The loss in grain quality from rust is reflected directly on car-inspection gradings. In 1933, a rust-free year, 87.3% of the cars inspected in the Western Grain Division were graded 1 Manitoba Hard, 1 Manitoba Northern, and 2 Manitoba Northern; while in 1935, a bad rust year, only 44.8% of the total number of cars inspected was of sufficiently high quality to be placed in the three top grades.

It was estimated that, due to reduction in grain quality from rust, the value of the wheat crop of Manitoba and Saskatchewan was reduced \$2,070,400 annually during the 11-year period 1925-1935. Although it has not been calculated, the loss in rust years due to low-grade oats of poor market value is very considerable.

Crop loss estimates based on the results of controlled experiments place the total annual loss from stem rusts of wheat and oats in Manitoba and Saskatchewan at \$34,895,400. A conservative estimate of the average annual loss caused by all cereal rusts in the three prairie provinces of Canada is \$40,000,000. This loss from cereal rusts is a factor of great economic importance to Western Canada.

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Résumé

Pertes causées par la rouille des céréales dans l'ouest du Canada, F. J. Greaney, Laboratoire fédéral de recherches sur la rouille, Winnipeg, Man.

Se basant sur les résultats d'expériences contrôlées, l'auteur estime que pendant la période de onze années, de 1925 à 1935, la rouille de la tige a prélevé annuellement un tribut de 10.8 pour cent sur le rendement possible de la récolte de blé dans les provinces du Manitoba, et de la Saskatchewan. Ceci représente une perte de 35,518,000 de boisseaux dont la valeur atteint le montant imposant de \$30,784,000. Pendant les six années 1929-1935 la perte moyenne annuelle subie par la récolte d'avoine au Manitoba et en Saskatchewan a été de 5.5 pour cent du rendement possible, soit 8,334,000 de boisseaux. Il en est résulté que le revenu annuel des producteurs de grain a été réduit de \$2,041,000. Les pertes causées par la rouille n'ont pas été computées pour l'Alberta. Une autre source importante de dégâts causés par la rouille est la détérioration de la qualité du grain qui abaisse sa valeur marchande et dont il faut tenir compte tout autant que de la diminution du rendement. La détérioration causée par la rouille est révélée par les catégories dans lesquelles le grain est classé à l'inspection des wagons. En 1933, une année sans rouille, 87.3 pour cent des wagons inspectés dans la Division de grain de l'Ouest a été classé 1 dur du Manitoba, 1 Nord du Manitoba et 2 Nord du Manitoba, tandis qu'en 1935, une année de forte rouille, la proportion des wagons inspectés ayant une qualité suffisante pour être classés dans les trois catégories supérieures n'était que de 44.8 p.c. du total. On estime qu'en raison de la détérioration de la qualité du grain par la rouille la valeur de la récolte de blé du Manitoba et de la Saskatchewan a été réduite de \$2,070,400 tous les ans pendant la période de 11 années, de 1925 à 1935. La perte causée par la détérioration dans la valeur marchande de l'avoine dans les années de rouille n'a pas été calculée, mais la perte est très considérable. Les évaluations basées sur les résultats d'expériences contrôlées portent la perte totale annuelle causée par les rouilles de la tige du blé et de l'avoine au Manitoba et en Saskatchewan à \$34,895,400. Une évaluation modérée de la perte moyenne annuelle causée par toutes les rouilles des céréales dans les trois provinces des Prairies du Canada est de \$40,000,000. Cette perte causée par les rouilles des céréales est un facteur de grande importance économique dans l'Ouest du Canada.

EXPERIMENTS ON THE CHEMICAL CONTROL OF SNOW-MOULD OF TURF IN ALBERTA¹

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During recent years snow-mould has caused considerable damage to turf on golf courses, bowling greens, and lawns in Alberta. Although Monteith (1) studied this disease and its control in the United States, it seemed advisable to determine the efficacy of these control methods under the climatic conditions of Alberta.

SYMPTOMS

Usually the first symptoms of snow-mould injury appear in the form of dead areas of turf of various shapes and sizes as the snow melts in early spring. The most common shape is circular in outline. Damage may also occur during late fall and early winter in Alberta, if the snow is melted by Chinook winds or otherwise. This happened at Edmonton and Calgary in 1933 and 1934. The hyphae of the fungi which are associated with the killing of grass in these dead areas are often abundant in or on the melting snow or ice, since they grow well at such low temperatures. The degree of injury depends upon whether the causal fungi operate more or less superficially on the grass, or whether extensive penetration of the crown and root areas occurs.

An excellent opportunity to study chemical methods of control was provided at the Mayfair Golf and Country Club, Edmonton, where unused greens were loaned for experimental treatment. This study was supplemented by information obtained from control measures employed at four other golf courses at Edmonton during the same period, and also from several courses at other points in Alberta.

CAUSAL FUNGI

No attempt was made to ascertain the relative prevalence of various fungi which might be associated with the killing of the turf in a given case. However, surface disinfected portions of the crown and roots of killed grass plants yielded, when incubated at 10° and 24° C. on nutrient agar, a *Fusarium* sp., a *Rhizoctonia* sp., and frequently an unidentified basidiomycetous fungus with characteristic clamp connections. Pathogenicity tests made at 6° C. indicated that on Chewing's fescue (*Festuca rubra* var. *Fallax*) the *Fusarium* isolate, and also the basidiomycete were both fairly pathogenic, and that the *Rhizoctonia* isolate caused only slight injury. In making the tests, the inoculum of each fungus, increased on oat hulls, was scattered over the plants after they had grown at room temperature in initially sterilized soil for one month. Only one isolate of each fungus indicated was tested for pathogenicity, and the species in each case was not determined.

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TEMPERATURE STUDIES

Petri plates, containing potato dextrose agar, were planted with the three organisms mentioned, and five plates of each isolate were distributed in incubators held at 0°, 6°, 15°, 20°, 25° and 30° C., respectively. All isolates grew fairly well at temperatures from 0° to 6° C. Both the *Fusarium* and the *Rhizoctonia* isolates grew best at 20°–25° C. The basidiomycete developed best between 6° and 15° C., and ceased growth at 20° C.

EXPERIMENTS ON CONTROL OF SNOW-MOULD WITH CORROSIVE SUBLIMATE AND CALOMEL

At the Mayfair Golf and Country Club, Edmonton, two recently abandoned greens were provided for experimental use. On these the efficiency of calomel and corrosive sublimate, applied at different rates, alone and in various proportions, was tested. The rates used were 1, 2, 3, . . . up to 10 ounces per 1,000 square feet, and the proportions of corrosive sublimate to calomel were: 4 : 0; 3 : 1; 2 : 2; 1 : 3; 0 : 4, respectively. The plots, each ten feet square, were separated by two-foot alleys. Finely ground chemicals were thoroughly mixed with sharp, dry sand in a quart Mason jar. This mixture was spread evenly on the turf. The plots were watered lightly after each treatment.

Rate and Proportion

The different rates and proportions of corrosive sublimate to calomel, indicated above, were applied to the experimental plots October 2, 1933. Two weeks later slight injury to the turf was evident only where corrosive sublimate was used alone at the 9 and 10 ounce rates. However, with the advent of spring this injury had apparently disappeared.

Snow-mould was abundant during November and the following April on the fairways and on the untreated portions of the putting greens. Some injury was also noticeable on all of the experimentally treated areas which received the 1 and 2-ounce rates of either calomel or corrosive sublimate, or various proportions of these. A trace of snow-mould developed on those plots which received calomel only at the 3-ounce rate, but it did not occur where larger quantities were applied. Finally, there was control from the 3-ounce and higher rates of corrosive sublimate, when used alone or where it was mixed with calomel in any of the proportions mentioned.

Injury to turf from the chemical

Another experiment was designed to determine the severity of injury to turf from different amounts of corrosive sublimate and calomel. Five applications were made every seventh day, beginning June 29, 1933. The rates were 1, 2, 3, 4, and 5 ounces per 1,000 square feet, and the proportions of corrosive sublimate to calomel were 4 : 0; 3 : 1; 2 : 2; 1 : 3; and 0 : 4. The turf was lightly watered after each application. Thus, some of the plots received as much as 25 ounces of chemical per 1,000 square feet of turf in one month, or an amount equal to that necessary for practical control during five or six years. In spite of this, there was no distinct evidence of chemical injury, either at this time or later.

Are yearly applications necessary?

In the series of plots which received the five weekly applications during July, 1933, another and final treatment was given on October 2,

1933. This experimental area was treated exactly as the other greens on the golf course with regard to watering, clipping and fertilizing throughout 1933 and 1934. Another area received four ounces per 1,000 square feet, of two parts of calomel to one part of corrosive sublimate in the falls of 1933 and 1934. In November 1934, and April 1935, snow-mould developed abundantly at random on the plots treated in 1933 only, being almost as severe as it was on those which received no treatment. Snow-mould did not develop on any of the areas treated each year. The necessity of treating each year was further emphasized at one of the Edmonton golf clubs where, as an economy measure in the fall of 1934, the greens were not treated and severe injury developed. So striking were the results that there appears little doubt as to the necessity of treating turf each year to obtain control. These studies also indicated that nothing is to be gained by applying more chemical than is necessary for the practical control of snow-mould during a given season.

PRACTICAL CONTROL MEASURES

The Chemical

As indicated previously, practical control of snow-mould was obtained by the use of calomel and corrosive sublimate in any proportion, provided the rate was four ounces or greater per 1,000 square feet. However, it seemed advisable to recommend equal parts of corrosive sublimate and calomel, because this mixture would provide immediately available toxicity from the corrosive sublimate to control a fall attack of snow-mould, and it would also possess, due to its slower oxidation, the lasting qualities of the calomel to combat the early spring attack.

Applying the Chemical

Whether the chemical is applied by means of a machine or by a shovel, it should first be mixed thoroughly with a small amount of dry, sharp sand. With this should be mixed enough additional sand, or dry earth compost, to ensure an even distribution of the chemical. Wire mats should be dragged both ways across the turf immediately after treatment. If these directions are observed and the amount of chemical does not fall below four ounces per 1,000 square feet of turf, satisfactory results should follow. At least this possibility has been demonstrated at the various golf clubs at Edmonton and at other points in Alberta.

SUMMARY

A *Fusarium* sp., a *Rhizoctonia* sp., and an unidentified basidiomycete were found constantly associated with snow-mould injury of turf on golf greens at Edmonton. As a representative isolate of each fungus was pathogenic at 6° C. to *Festuca rubra* var *fallax*, it is concluded that any one or all three of the fungi indicated, acting alone or together, may cause turf injury in Alberta.

As much as eight ounces of either corrosive sublimate or calomel, or various proportions of these, applied to 1,000 square feet of turf, did not cause noticeable injury when the turf was lightly watered following application.

Either calomel or corrosive sublimate is an effective control of snow-mould, if not less than four ounces per 1,000 square feet are used.

Because of the possible incidence of snow-mould in the fall, a suitable formula for Alberta should consist of equal parts of corrosive sublimate and calomel. This applied in the fall at the rate of four ounces per 1,000 square feet of turf should give satisfactory control.

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Résumé

Expériences sur le traitement chimique de la moisissure des neiges du gazon dans l'Alberta. W. C. Broadfoot, laboratoire fédéral de phytopathologie, Edmonton, Alberta.

Une espèce de *Fusarium*, une espèce de *Rhizoctonia* et un cryptogame basidiomycète non identifié à pinces caractéristiques, ont été isolés d'un gazon infesté de moisissure des neiges, et se sont montrés pathogéniques pour *Festuca rubra* var. *Fallax* à 6° C. Les deux premiers organismes ont atteint leur meilleur développement à 20°-25° C., tandis que le dernier l'a fait entre 6° et 15° C., et a cessé de végéter à 20° C. Une quantité allant jusqu'à 8 onces par 1,000 pieds carrés de sublimé corrosif ou de calomel ou de différentes proportions de ces ingrédients, n'a pas causé de dommages apparents, lorsque le gazon était légèrement arrosé après les applications. Comme il est possible que la moisissure des neiges fasse son apparition en automne aussi bien qu'au printemps, une bonne formule pour l'Alberta paraît être celle qui se compose de parties égales de sublimé corrosif et de calomel, appliqués en automne à raison de quatre onces par 1,000 peids carrés de gazon.

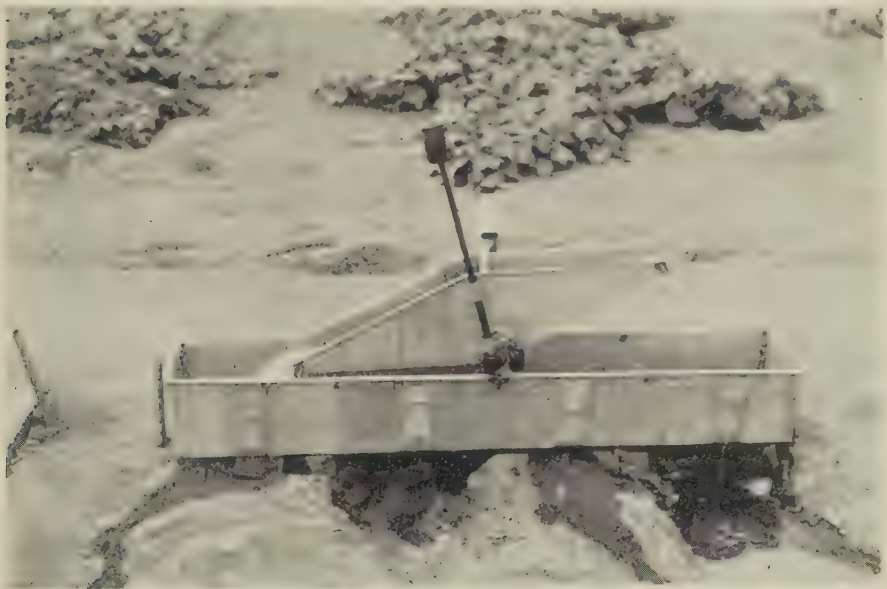
A MEASURING DEVICE FOR IRRIGATION EXPERIMENTS¹

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A simple yet practical and efficient device for measuring irrigation water applied to individual rows has been developed at the Summerland Experimental Station. This device may be used where water can be delivered into it from standpipes or hose or by gravity from a carrier flume at least 2 feet from the ground. The apparatus consists of a delivery box, a rocker box, a balance rod and weight, and a counter.



Irrigation Measuring Device in Operation

Delivery Box

The delivery box consists of a galvanized iron box 48 inches long, 8 inches wide and $6\frac{1}{2}$ inches deep. The edges are reinforced with $\frac{1}{4}$ -inch bar iron rods over which the edge of the galvanized iron is closely rolled. Four holes, each $1\frac{1}{4}$ inches in diameter, are cut at 6 inches and 18 inches from the ends. These are opened or closed by close-fitting sliding metal gates which slide in grooves soldered to the sides of the box. Across the top of the box at its centre is placed a rocker support. A piece of strap iron, $1\frac{1}{4}$ inches wide by 12 inches long, is bolted at each end to clips soldered to the sides of the box. This is dropped $\frac{3}{4}$ of an inch below the top of the box by right angled bends $2\frac{1}{2}$ inches each side of the centre. Cross bars made of $\frac{1}{4}$ -inch rods are placed 12 inches each side of the centre and $\frac{1}{2}$ inch

¹ Contribution from the Division of Horticulture, Experimental Farms Branch.

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below the top of the box. These are threaded at the ends and held in place by nuts. A piece of $\frac{1}{2}$ -inch rubber garden hose, $7\frac{1}{2}$ inches long, is placed on each cross bar.

Rocker Box

The rocker box consists of a galvanized iron box constructed as shown in the illustration. The edges are each 15 inches from the centre of the rocker bar to the end. The width is $4\frac{1}{4}$ inches. The inside depth is $7\frac{1}{2}$ inches with a 1-inch lip at each end. The upper edges and also the edges of the lip are reinforced by rolling over No. 9 copper wire. The rocker box is supported by a rod $\frac{3}{8}$ of an inch in diameter the ends of which pass through holes bored in the strap iron midway in each $\frac{3}{4}$ -inch drop. A cradle consisting of a galvanized iron tube slightly larger than the $\frac{3}{8}$ -inch rod is soldered to the bottom of the rocker box by flaring edges. The rocker box is divided into two parts by a water-tight galvanized iron partition soldered firmly to the sides of the rocker box at the centre. The top of this partition is reinforced by rolling the edge over No. 9 wire. On the front of the rocker box exactly at the centre, two clips of heavy galvanized iron are riveted in place to support the balance rod. A metal clip to trip the counter is riveted to the side of the rocker box.

Balance Rod and Weight

The balance rod consists of a piece of $\frac{1}{2}$ -inch iron rod, 18 inches in length. A 2-inch cube of iron is drilled so that the $\frac{1}{2}$ -inch rod will slide through it and a set screw is placed in the side of the cube to tighten against the rod and hold the weight at the desired height.

Counter

A Veeder-Root Hand Tally reset counter is attached to a metal clip on the end of the strap iron rocker box support in such a position that the clip on the side of the rocker box will press the lever as the box tips to the side where the counter is placed.

Operation

When the weight on the balance rod is approximately 12 inches from the bottom, one side of the rocker box will hold approximately one-half gallon. The weight should be adjusted until each side will deliver exactly one-half gallon measured with an Imperial gallon measure. Water is allowed to run into one side of the rocker box until it tips to one side and delivers one-half gallon into the delivery box. While delivery is taking place, the water runs into the other side of the rocker box. When this side is full, the rocker box tips back to its original position delivering another half gallon and at the same time registering one gallon on the counter. Distribution may be made from the delivery box by opening any of the gates desired. The water delivered is recorded in gallons. As $6\frac{1}{4}$ Imperial gallons equal 1 cubic foot, the volume of water delivered can readily be converted to cubic feet. The depth of application can then be determined by dividing the volume in cubic feet by the area of the plot.

It has been found advisable to deliver the water to the top of the rocker box by means of a curved spout, the end of which will just clear the rocker box. This prevents strong winds from blowing the water over the side of the box. The jar of the rocker box as it tips and strikes the cross bar may move the delivery box unless the latter is firmly fastened in place.

BOOK REVIEWS

INSECT ENEMIES OF SHADE-TREES by Glen W. Herrick, Professor of Economic Entomology in Cornell University, Ithaca, New York; Comstock Publishing Co., Inc. Price \$5.00.

Professor Herrick is to be congratulated for bringing out another very useful volume. Chapter I discusses the value of shade-trees and general methods of protection from insect attack; II, the materials and apparatus for the control of tree and shrub insects; III, suggestions for the treatment of weakened trees; and chapters IV to XXVII, the insect enemies of ash, beech, birch, buckeye, horsechestnut, catalpa, elm, ginko, hackberry, hickory, larch, linden, locust, magnolia, maple, mountain ash, oak, pine, poplar, sycamore, tree-of-Heaven, tulip, tupelo, sweet gum, walnut and willow. Chapter XXVIII treats of insect enemies of smaller trees and shrubs, XXIX of evergreens other than pines, and XXX, of some miscellaneous insect enemies of trees and shrubs.

This volume of 417 pages and 321 illustrations, discusses the large number of insect species which attack shade-trees in the United States and Canada. Under each species, following the description of the insect, information is given regarding its life history, the injury caused and the methods of control. In most instances, references are given to important papers published by other authors.

The printing of the book is pleasing, the illustrations have been well chosen, and the text contains a wealth of information for all who are interested in the welfare of our shade-trees, whether in cities, along roadways, or on private grounds.

ARTHUR GIBSON.

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PLANT BREEDING ABSTRACTS, SUPPLEMENT II. (Summary of Reports received from stations in the British Empire 1932-35). Imperial Bureau of Plant Genetics (For crops other than herbage). School of Agriculture, Cambridge, England.

This Supplement to Plant Breeding Abstracts which has been compiled from the annual reports received at the Imperial Bureau of Plant Genetics, Cambridge, is intended to give a concise account of the work on plant breeding and related topics in the British Empire during 1932-35 and one which will be at the same time in a convenient form for reference. The amount and range of plant breeding work in the British Empire is of course enormous and the publication has involved the scrutiny of over 400 reports.

Much of the work referred to is only available in annual reports, being more or less of a routine nature, and but for the activity of the Imperial Bureau of Plant Genetics would have remained inaccessible to the general reader. Another valuable feature of the Supplement is that many of the items included concern work which though likely to be published in the future has not yet reached that stage.

The crops dealt with cover practically the whole range of economic plants with the exception of herbage plants and the work reported includes breeding, genetics and cytology. There is also a section on the genetics of plant parasites.

The Supplement is very comprehensive and is planned in such a way that the work on a given crop in a given country can be turned up at once; an extensive index is also provided.

Reviews of this kind are invaluable to practical breeders in giving a survey of the work in progress in the whole field of plant breeding and should be read with interest also by all those interested in modern genetics and its application to agricultural plants.

A similar supplement is in process of compilation from the reports received from foreign stations.

HUMUS, ORIGIN, CHEMICAL COMPOSITION AND IMPORTANCE IN NATURE. By Selman A. Waksman, Professor of Soil Microbiology, Rutgers University, and Microbiologist, New Jersey Agricultural Experiment Station. Published by The Williams & Wilkins Company, Baltimore, U.S.A. Price \$6.50.

In this excellent work "Humus is treated as a natural body produced universally in nature, wherever plant and animal residues are undergoing decomposition." Dr. Waksman emphasizes the primary rôle of micro-organisms, yet he does not overlook the importance of chemical reactions and he uses the terminology of chemistry and of soil science. He deals with his subject under three main heads:— A. The historical development of our present knowledge of the chemical nature of humus, its formation and its rôle in plant nutrition; B. The origin and chemical nature of humus as it is found in composts, animal manures and green manures, in forest and heath soils, in peats and mucks, in the different classes of mineral soils—field, grass-land, garden and orchard—and in water systems; C. The relationships of humus and its constituent substances in agriculture and in soil science, and its analysis.

The book will be found useful as a source of references, with its bibliography of 1311 citations. It will be particularly valuable to advanced students of soil science and should find a place in all libraries which cover that subject. Dr. Waksman's leading position and long experience in the field have helped him to deal with this difficult subject in a masterly way. If any criticism of the book is warranted perhaps it is that there is not enough definite statement of the author's own opinions. From such an undoubted authority as Waksman we might expect more discussion of debatable points and more expression of personal opinion. This modesty, however, does not lessen the book's value and it will rightly occupy the leading position in this field. A well-written monograph of this sort, on a subject so widely studied and in a field of knowledge so rapidly being added to, should be kept up-to-date, and it is to be hoped that new editions will be forthcoming in due course.

The book is admirably indexed and the chapters are excellently presented. As in any great work of this kind a few mistakes in reference material occur but there are not many. One minor error that has come to this reviewer's attention is found on page 150. There is credited to W. L. Davies the demonstration of the presence of dinucleotides in peat humus, whereas in his paper to which reference is made Davies merely cites the paper of W. B. Bottomley on "Isolation from Peat of certain Nucleic Acid Derivatives," which appear in Proc. Royal Soc. (London) B 90, 1917, which paper by Bottomley is cited elsewhere in Waksman's book.

In reading the book through one is impressed by the writer's thorough grasp of his subject and by the fact that it is written by a man who is himself a laboratory man yet *au fait* with field conditions, and a scientific producer of new thought and new knowledge.

R. R. McKIBBIN.

BREEDING PROFITABLE DAIRY CATTLE. E. Parmalee Prentice. Houghton Mifflin Company, Boston, Mass., U.S.A. Price \$2.50.

When this reviewer began getting instruction in agriculture nearly fifty years ago, there were very few text books that were suitable for school or college use. Since that time and especially in the last twenty years, a great many handbooks for the farmer have been written. Some of these are excellent books; others are merely paper and ink.

A new book has just come to my desk that is of special interest and value to the farmer. It is entitled, "Breeding Profitable Dairy Cattle" and was written by E. Parmalee Prentice, owner of Mount Hope Farm, Williamstown, Mass. Mr. Prentice seeks to apply our modern knowledge of genetics to the breeding of

dairy cattle. He believes that present distress is not due to "agriculture in itself." "It is true that agriculture has made progress in the twentieth century, but other industries have made vastly greater progress, and as compared with other spheres of human effort, agriculture is far behind." He states further, "Improvement of agriculture depends, then, upon efficiency in breeding and managing livestock."

Mr. Prentice discusses in a very entertaining manner the history of livestock farming. He divides it into four periods. 1st, Old Time Farming; 2nd, The Story of the Dutch Breed; 3rd, The Influence of Herd Books, and 4th, Cow Testing Associations. Many interesting and instructive comparisons are made between ancient and modern methods. In some cases old methods are not inferior to new.

The whole argument of the first eight chapters leads up to the statement that the method of selection of breeding stock has been extremely faulty. Selection by type has not been successful. "So far as type is concerned, it is well known that between form and function no relation has yet been found that enables a breeder, by inspection, to distinguish between bulls which do and bulls which do not transmit high production to their daughters." Furthermore, selection by pedigree has not proved successful. "As ordinarily made up, pedigrees of dairy cattle are genealogical tables merely, showing, with much irrelevant matter, the Advanced Registry records of some of the dams whose names appear on the sheet. This information is so incomplete as to be almost valueless."

The author is definitely critical of present methods of registering live stock. He claims that no advance can be made by admitting animals to registration simply because their sires and dams were registered.

All this is leading up to the recommendation of the Mount Hope index as an effective method of selecting bulls. This index is obtained by comparing the production of daughters of a certain bull with the production of their dams. "The simpler method of computing indices is illustrated as follows. . . . If the average mature equivalent of the dam's production is 8,000 pounds of milk and the daughters average mature equivalent is 10,000 lbs., the bull is a 12,000 pound bull. . . . If the average mature equivalent of the dam's production is 10,000 pounds of milk, the the daughter's average mature equivalent is 8,000 pounds of milk, the bull is a 6,000 pound bull." In the same way the index for butterfat test can be worked out.

Mr. Prentice is positive that by thus selecting bulls for productive ability, great progress can be made in the improvement of dairy cattle. His whole book is an interesting, challenging discussion of the dairy cattle problem. It should certainly be in the hands of, and carefully read by all breeders, and especially by breeders of dairy cattle.

J. M. TRUEMAN.

